MycoKeys 110: 67–92 (2024)
DOI: 10.3897/mycokeys.110.133108

Research Article

Morphological and molecular identification for four new wood-inhabiting species of *Lyomyces* (Basidiomycota) from China

Qi Yuan[1,2], Yunchao Li[2], Yunfei Dai[2], Kunyan Wang[2], Yixuan Wang[3], Changlin Zhao[1,2]

1 *The Key Laboratory of Forest Resources Conservation and Utilization in the Southwest Mountains of China Ministry of Education, Key Laboratory of National Forestry and Grassland Administration on Biodiversity Conservation in Southwest China, Yunnan Provincial Key Laboratory for Conservation and Utilization of In-forest Resource, Southwest Forestry University, Kunming 650224, China*
2 *College of Forestry, Southwest Forestry University, Kunming 650224, China*
3 *Yunnan Yunzhihuang Health Technology Co., LTD, Kunming 650224, China*
Corresponding author: Changlin Zhao (fungi@swfu.edu.cn)

Abstract

Fungi are one of the most diverse groups of organisms on Earth, in which the wood-inhabiting fungi play an important role in forest ecosystem processes and functions. Four new wood-inhabiting fungi, *Lyomyces hengduanensis*, *L. niveomarginatus*, *L. wumengshanensis* and *L. zhaotongensis*, are proposed, based on morphological features and molecular evidence. *Lyomyces hengduanensis* differs in the brittle basidiomata with pruinose hymenial surface, a monomitic hyphal system and ellipsoid basidiospores (3.5–6 × 3–4.5 µm). *Lyomyces niveomarginatus* is distinguished by the subceraceous basidiomata with crackled hymenial surface, a monomitic hyphal system and ellipsoid basidiospores (4.5–7 × 3–4 µm). *Lyomyces wumengshanensis* is distinguished by the grandinioid hymenial surface, a monomitic hyphal system and ellipsoid to broad ellipsoid basidiospores (4–6 × 3–5 µm). *Lyomyces zhaotongensis* is unique in the grandinioid hymenial surface, a monomitic hyphal system and broadly ellipsoid basidiospores measuring as 2.6–3.5 × 2.5–3 µm. Sequences of ITS and nLSU rRNA markers of the studied samples were generated and phylogenetic analyses were performed using the Maximum Likelihood, Maximum Parsimony and Bayesian Inference methods. The phylogram, based on the ITS+nLSU rDNA gene regions, included three genera within the Schizoporaceae viz. *Fasciodontia*, *Lyomyces* and *Xylodon*, in which the four new species were grouped into *Lyomyces*. The phylogenetic tree inferred from the ITS sequences highlighted that *L. hengduanensis* group with *L. zhaotongensis* and then closely grouped with *L. crustosus*, *L. ochraceoalbus*, and *L. vietnamensis*. The new taxon *L. niveomarginatus* was retrieved as a sister to *L. juniperi*. The new species *L. wumengshanensis* was sister to *L. macrosporus*. The new taxon *L. zhaotongensis* grouped with *L. hengduanensis* and then closely grouped with *L. crustosus*, *L. ochraceoalbus* and *L. vietnamensis*.

Key words: Biodiversity, phylogenetic analyses, taxonomy, Yunnan Province

OPEN ACCESS

This article is part of:
Exploring the Hidden Fungal Diversity: Biodiversity, Taxonomy, and Phylogeny of Saprobic Fungi
Edited by Samantha C. Karunarathna, Danushka Sandaruwan Tennakoon, Ajay Kumar Gautam

Academic editor:
Samantha C. Karunarathna
Received: 25 July 2024
Accepted: 15 October 2024
Published: 30 October 2024

Citation: Yuan Q, Li Y, Dai Y, Wang K, Wang Y, Zhao C (2024) Morphological and molecular identification for four new wood-inhabiting species of *Lyomyces* (Basidiomycota) from China. MycoKeys 110: 67–92. https://doi.org/10.3897/mycokeys.110.133108

Introduction

Fungi are one of the most diverse groups of organisms on Earth and play an indispensable role in the forest ecosystem processes and functioning (Hyde 2022; Guan et al. 2023; Deng et al. 2024a). The wood-inhabiting fungal family

Schizoporaceae Jülich includes many variations of the fruiting body types within the order Hymenochaetales Oberw. (Larsson et al. 2006; Wu et al. 2022a; Guan et al. 2023; Zhang et al. 2024) and it comprises a number of representative wood-inhabiting fungal taxa, including diverse hymenophoral morphologies as hydnoid, corticioid and polyporoid (Yurchenko and Wu 2016; Riebesehl and Langer 2017; Yurchenko et al. 2017; Cui et al. 2019; Riebesehl et al. 2019; Jiang et al. 2021; Wu et al. 2022a, 2022b; Guan et al. 2023; Deng et al. 2024a, b; Zhang et al. 2024). In addition, taxa of the family Schizoporaceae are widely found in different continents, causing white rot (Langer 1994; Luo et al. 2022; Guan et al. 2023; Zhang et al. 2024).

The genus *Lyomyces* P. Karst. is typified by *L. sambuci* (Pers.) P. Karst. It is characterised by the resupinate-to-effused basidiomata with a smooth-to-odontioid hymenophore, a monomitic hyphal system with generative hyphae bearing clamp connections, the presence of several types of cystidia and with smooth, thin- to slightly thick-walled basidiospores (Karsten 1881; Bernicchia and Gorjón 2010). Based on the MycoBank database (http://www.mycobank.org, accessed on 25 April 2024) and the Index Fungorum (http://www.indexfungorum.org, accessed on 25 April 2024), *Lyomyces* has 55 specific and infraspecific names registered, of which approximately 41 species of *Lyomyces* are currently known (Rabenhorst 1851; Karsten 1881; Karsten 1882; Cunningham 1959; Cunningham 1963; Wu 1990; Hjortstam and Ryvarden 2009; Xiong et al. 2009; Dai 2010; Dai 2011; Yurchenko and Wu 2013; Gafforov et al. 2017; Riebesehl and Langer 2017; Yurchenko et al. 2017; Chen and Zhao 2020; Yurchenko et al. 2020; Luo et al. 2021b; Luo et al. 2021c; Viner et al. 2022; Guan et al. 2023).

On the basis of the frequent inclusion of data from DNA sequences in many phylogenetic studies, the classification of the wood-inhabiting fungi has been updated continuously (Yurchenko et al. 2020). These pioneering research studies into the family Schizoporaceae were just the prelude to the molecular systematics period (Guan et al. 2023; Zhang et al. 2024). The genus *Hyphodontia* s.l. was indicated to be a polyphyletic group, in which the genera *Xylodon* (Pers.) Gray and *Kneiffiella* P. Karst. included the largest number of species (Yurchenko and Wu 2016; Riebesehl and Langer 2017; Riebesehl et al. 2019). Due to the lack of sequences of some wood-inhabiting fungal taxa, it is difficult to clearly distinguish many genera in this family Schizoporaceae using molecular data; therefore, a broad concept of *Hyphodontia* s.l. was accepted (Yurchenko and Wu 2016; Riebesehl and Langer 2017; Wang and Chen 2017; Riebesehl et al. 2019). Based on the nuclear DNA sequence data, six well-distinguished clades as *Hastodontia* clade, *Hyphodontia* clade, *Lagarobasidium* clade, *Kneiffiella-Alutaceodontia* clade, *Xylodon-Lyomyces-Rogersella* clade and *Xylodon-Schizopora-Palifer* clade, were included, based on the phylogenetical studies for *Hyphodontia* s.l., in which the genus *Lyomyces* was nested within the *Xylodon-Lyomyces-Rogersella* clade (Yurchenko and Wu 2013). The research revealed that *Hyphodontia* s.l. was divided into six genera, viz., *Hastodontia* (Parmasto) Hjortstam & Ryvarden, *Hyphodontia* J. Erikss., *Kneiffiella*, *Lagarobasidium* Jülich, *Lyomyces* and *Xylodon*, in which 35 new combinations were proposed, including fourteen *Lyomyces* species (Riebesehl and Langer 2017). On the basis of the sequences of the internal transcribed spacer (ITS) and the nuclear large subunit (nLSU) ribosomal DNA gene, the phylogenetic analysis clarified that the *Lyomyces sambuci* complex divided into four new

species (Yurchenko et al. 2017). Riebesehl et al. (2019) clarified the generic concept and their phylogenetic reconstruction of *Lyomyces* and the species *L. sambuci* was sister to *L. crustosus* (Pers.) P. Karst (Riebesehl et al. 2019). Based on a combination of the morphological and molecular evidence, the fungal diversity of the family Schizoporaceae was analysed, in which six new species were described: *L. fissuratus* C.L. Zhao, *L. fumosus* C.L. Zhao, *L. niveus* C.L. Zhao, *L. ochraceoalbus* C.L. Zhao, *L. albopulverulentus* C.L. Zhao and *L. yunnanensis* (Luo et al. 2021b, 2021c; Guan et al. 2023).

During the investigations of the wood-inhabiting fungi, we collected four new Hymenochaetales taxa from Yunnan Province, China, that could not be assigned to any described species of the order. We present the morphological characteristics and phylogenetic analyses with ITS and nLSU that support the four species in the genus *Lyomyces*.

Materials and methods

Morphology

Fresh basidiomata of the fungi growing on the angiosperm branch were collected from the Honghe, Lincang, Puer, Wenshan and Zhaotong of Yunnan Province, P.R. China after recording important information (Rathnayaka et al. 2024). Specimens were dried in an electric food dehydrator at 40 °C (Hu et al. 2022), then sealed and stored in an envelope bag and deposited in the Herbarium of the Southwest Forestry University (SWFC), Kunming, Yunnan Province, P.R. China. Macromorphological descriptions were based on field notes and photos were captured in the field and lab. Colour terminology follows Petersen (Petersen 1996). Micromorphological data were obtained from the dried specimens when observed under a light microscope following the previous study (Guan et al. 2023). The following abbreviations are used: KOH = 5% potassium hydroxide water solution, CB = Cotton Blue, CB– = acyanophilous, IKI = Melzer's Reagent, IKI– = both inamyloid and indextrinoid, L = mean spore length (arithmetic average for all spores), W = mean spore width (arithmetic average for all spores), Q = variation in the L/W ratios between the specimens studied and n = a/b (number of spores (a) measured from given number (b) of specimens).

Molecular phylogeny

The EZNA HP Fungal DNA Kit (Omega Biotechnologies Co., Ltd., Kunming, China) was used to extract DNA with some modifications from the dried specimens. The nuclear ribosomal ITS region was amplified with primers ITS5 and ITS4 (White et al. 1990). The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 58 °C for 45 s and 72 °C for 1 min and a final extension of 72 °C for 10 min. The nuclear nLSU region was amplified with primer pair LR0R and LR7 (Rehner and Samuels 1994). The PCR procedure for nLSU was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 48 °C for 1 min and 72 °C for 1.5 min and a final extension of 72 °C for 10 min. The PCR procedure for ITS and nLSU followed the previous study (Zhao and Wu 2017). All newly-generated sequences were deposited in NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/) (Table 1).

Table 1. List of species, specimens, and GenBank accession numbers of sequences used in this study.

Species name	Specimen No.	GenBank accession No.		References
		ITS	nLSU	
Fasciodontia brasiliensis	MSK-F 7245a	MK575201	MK598734	Yurchenko et al. (2020)
F. bugellensis	KAS-FD 10705a	MK575203	MK598735	Yurchenko et al. (2020)
F. bugellensis	MSK-F 7353	MK575205	MK598736	Yurchenko et al. (2020)
F. yunnanensis	CLZhao 6280	MK811275	MZ146327	Luo and Zhao (2021)
F. yunnanensis	CLZhao 6385	MK811277	–	Luo and Zhao (2021)
Hymenochaete ochromarginata	He 47	KU978861	JQ279666	Unpublished
H. rubiginosa	He 458	JQ279580	–	He and Li (2013)
Lyomyces albopulverulentus	CLZhao 21478	OP730712	OP730724	Guan et al. (2023)
L. allantosporus	KAS-GEL4933	KY800401	–	Yurchenko et al. (2017)
L. allantosporus	FR-0249548	KY800397	–	Yurchenko et al. (2017)
L. bambusinus	CLZhao 4831	MN945968	–	Chen and Zhao (2020)
L. bambusinus	CLZhao 4808	MN945970	–	Chen and Zhao (2020)
L. cremeus	CLZhao 4138	MN945974	–	Chen and Zhao (2020)
L. cremeus	CLZhao 8295	MN945972	–	Chen and Zhao (2020)
L. crustosus	TASM:YG G39	MF382993	–	Gafforov et al. (2017)
L. crustosus	UC2022841	KP814310	–	Unpublished
L. densiusculus	Ryvarden 44818	OK273853	–	Viner et al. (2022)
L. elaeidicola	LWZ20180411-20	MT319458	–	Wang et al. (2021)
L. elaeidicola	LWZ20180411-19	MT319457	–	Wang et al. (2021)
L. erastii	TASM:YG 022	MF382992	–	Gafforov et al. (2017)
L. erastii	23cSAMHYP	JX857800	–	Unpublished
L. fimbriatus	Wu910620-7	MK575209	–	Yurchenko et al. (2020)
L. fimbriatus	Wu911204-4	MK575210	–	Yurchenko et al. (2020)
L. fissuratus	CLZhao 4352	MW713742	–	Luo et al. (2021b)
L. fissuratus	CLZhao 4291	MW713738	–	Luo et al. (2021b)
L. fumosus	CLZhao 8188	MW713744	–	Luo et al. (2021b)
L. gatesiae	LWZ20180515-3	MT319447	–	Wang et al. (2021)
L. gatesiae	LWZ20180515-32	MT319448	–	Wang et al. (2021)
L. griseliniae	KHL 12971 (GB)	DQ873651	–	Larsson et al. (2006)
L. hengduanensis	CLZhao 20627	OR793233	PP657611	Present study
L. hengduanensis	CLZhao 25551	OR658999	PP657610	Present study
L. hengduanensis	CLZhao 32713	OR899153	–	Present study
L. hengduanensis	CLZhao 32714	OR899154	–	Present study
L. hengduanensis	CLZhao 32782	OR899155	PP657612	Present study
L. juniperi	FR-0261086	KY081799	–	Riebesehl and Langer (2017)
L. leptocystidiatus	LWZ20170818-1	MT326514	–	Wang et al. (2021)
L. leptocystidiatus	LWZ20170818-2	MT326513	–	Wang et al. (2021)
L. macrosporus	CLZhao 4516	MN945977	–	Chen and Zhao (2020)
L. mascarensis	KAS-GEL4833	KY800399	–	Yurchenko et al. (2020)
L. mascarensis	KAS-GEL4908	KY800400	–	Yurchenko et al. (2020)
L. microfasciculatus	CLZhao 5109	MN954311	–	Chen and Zhao (2020)
L. niveomarginatus	CLZhao 16360	PP537949	PP657607	Present study
L. niveus	CLZhao 6431	MZ262541	MZ262526	Luo et al. (2021b)
L. niveus	CLZhao 6442	MZ262542	MZ262527	Luo et al. (2021b)
L. ochraceoalbus	CLZhao 4385	MZ262535	MZ262521	Luo et al. (2021b)
L. ochraceoalbus	CLZhao 4725	MZ262536	MZ262522	Luo et al. (2021b)
L. ochraceoalbus	MSK7247	KY800403	–	Yurchenko et al. (2017)
L. orientalis	GEL3376	DQ340325	–	Yurchenko et al. (2017)
L. pruni	GEL2327	DQ340312	–	Larsson et al. (2006)
L. pruni	Ryberg 021018 (GB)	DQ873624	–	Larsson et al. (2006)
L. sambuci	KAS-JR7	KY800402	KY795966	Yurchenko et al. (2017)
L. sambuci	83SAMHYP	JX857721	–	Yurchenko et al. (2017)

Species name	Specimen No.	GenBank accession No.		References
		ITS	nLSU	
L. vietnamensis	TNM F9073	JX175044	–	Yurchenko et al. (2017)
L. wuliangshanensis	CLZhao 4108	MN945980	–	Chen and Zhao (2020)
L. wuliangshanensis	CLZhao 4167	MN945979	–	Chen and Zhao (2020)
L. wumengshanensis	CLZhao 29374	OR803021	PP657613	Present study
L. wumengshanensis	CLZhao 31486	OR899208	–	Present study
L. wumengshanensis	CLZhao 32705	OR899209	–	Present study
L. wumengshanensis	CLZhao 32736	OR899210	–	Present study
L. wumengshanensis	CLZhao 32800	OR899211	PP657614	Present study
L. wumengshanensis	CLZhao 32869	OR899212	–	Present study
L. wumengshanensis	CLZhao 32915	OR899213	PP657615	Present study
L. yunnanensis	CLZhao 2463	OP730711	OP730723	Guan et al. (2023)
L. yunnanensis	CLZhao 9375	OP730710	–	Guan et al. (2023)
L. yunnanensis	CLZhao 10041	OP730709	–	Guan et al. (2023)
L. zhaotongensis	CLZhao 32878	PP537950	PP657609	Present study
Xylodon afromontanus	H 7006811	OQ645463	–	Yurchenko et al. (2024)
X. asiaticus	CLZhao 10368	OM959479	–	Zhang et al. (2024)
X. cystidiatus	FR-0249200	MH880195	MH884896	Riebesehl et al. (2019)
X. daweishanensis	CLZhao 18492	OP730719	OP730727	Guan et al. (2023)
X. daweishanensis	CLZhao 18446	OP730717	OP730725	Guan et al. (2023)
X. filicinus	MSK-F 12869	MH880199	NG067836	Riebesehl et al. (2019)
X. fissuratus	CLZhao 7007	OP730713	–	Guan et al. (2023)
X. fissuratus	CLZhao 9407	OP730714	–	Guan et al. (2023)
X. hastifer	K(M) 172400	NR166558	–	Riebesehl and Langer (2017)
X. hyphodontinus	KAS-GEL9222	MH880205	MH884903	Riebesehl et al. (2019)
X. macrosporus	CLZhao 10226	MZ663809	MZ663817	Luo et al. (2021a)
X. puerensis	CLZhao 8142	OP730720	OP730728	Guan et al. (2023)
X. puerensis	CLZhao 8639	OP730721	OP730729	Guan et al. (2023)
X. quercinus	Larsson 11076 (GB)	KT361633	–	Larsson et al. (2004)
X. ramicida	Spirin 7664	NR138013	–	Unpublished
X. subflaviporus	Wu 0809-76	KX857803	–	Chen et al. (2017)
X. tropicus	CLZhao 3351	OL619261	OL619269	Qu et al. (2022)
X. wenshanensis	CLZhao 15729	OM338097	OM338104	Luo et al. (2022)
X. xinpingensis	CLZhao 11224	MW394662	MW394654	Luo et al. (2022)

The sequences were aligned in MAFFT version 7 (Katoh et al. 2019) using the G-INS-i strategy. The alignment was adjusted manually using AliView version 1.27 (Larsson 2014). The sequence alignments were deposited in figshare (DOI: 10.6084/m9.figshare.27166521). Sequences of *Hymenochaete ochromarginata* P.H.B. Talbot and *Hymenochaete rubiginosa* (Dicks.) Lév., retrieved from GenBank, were used as the outgroups in the ITS+nLSU analysis (Fig. 1). The sequence alignments were deposited in figshare (DOI: 10.6084/m9.figshare.27166521). Sequences of *Xylodon quercinus* (Pers.) Gray and *Xylodon ramicida* Spirin & Miettinen, retrieved from GenBank, were used as the outgroups in the ITS analysis (Fig. 2) (Guan et al. 2023; Zhang et al. 2024).

Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were applied to the combined three datasets following a previous study (Zhao and Wu 2017). All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1,000 random sequence additions. Max-trees were set to 5,000, branches of zero length were collapsed and all parsimonious trees were saved. Clade robustness was assessed using bootstrap

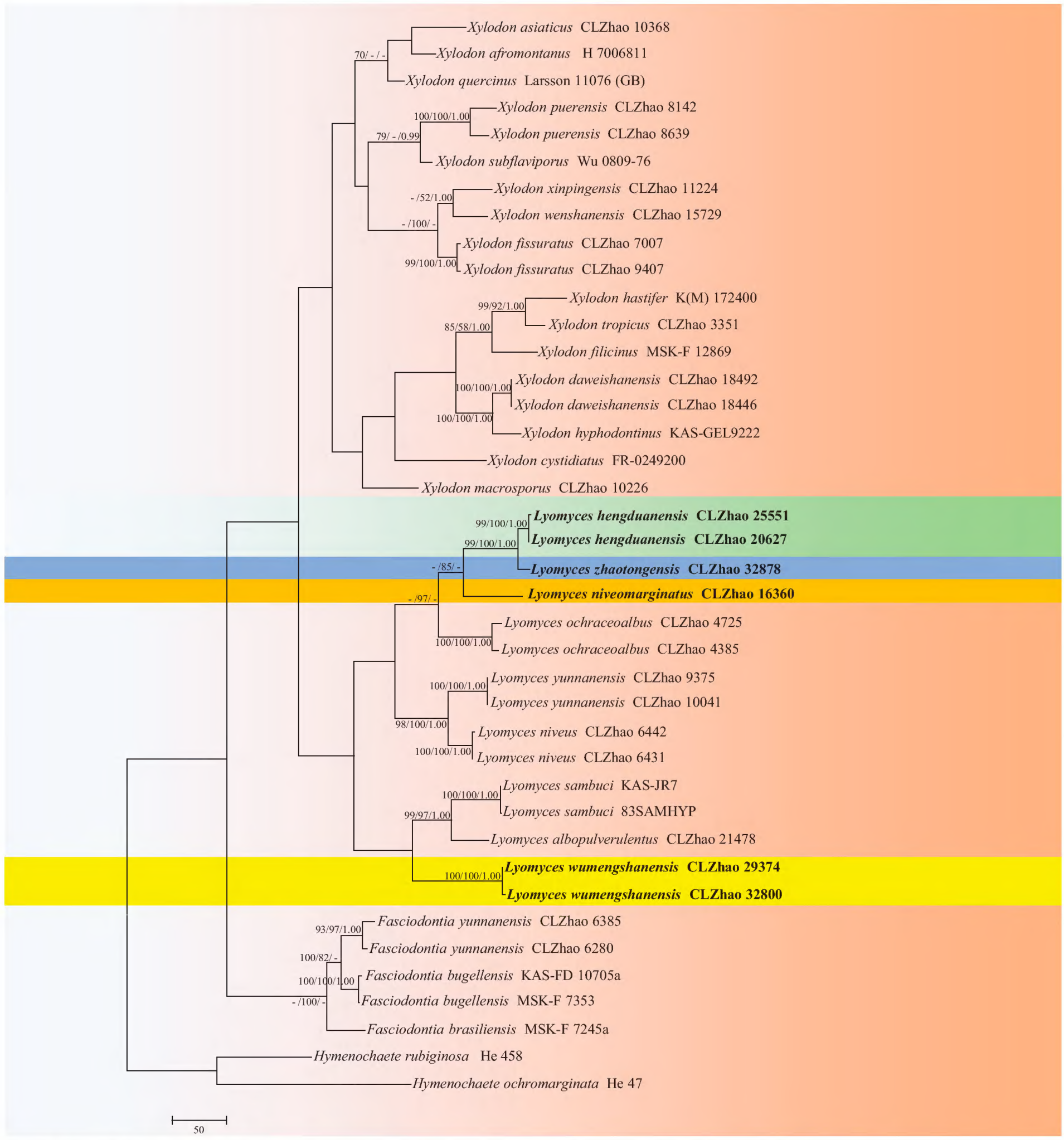

Figure 1. Maximum Parsimony strict consensus tree illustrating the phylogeny of four new species and related species in *Lyomyces* within Schizoporaceae, based on ITS+nLSU sequences. Branches are labelled with Maximum Likelihood bootstrap values ≥ 70%, parsimony bootstrap values ≥ 50% and Bayesian posterior probabilities ≥ 0.95, respectively.

(BT) analysis with 1,000 pseudo-replicates (Felsenstein 1985). Descriptive tree statistics - tree length (TL), composite consistency index (CI), composite retention index (RI), composite rescaled consistency index (RC) and composite homoplasy index (HI) - were calculated for each maximum parsimonious tree generated. The combined dataset was also analysed using Maximum Likelihood (ML) in RAxML-HPC2 through the CIPRES Science Gateway (Miller et al. 2012). Branch support (BS) for the ML analysis was determined by 1000 bootstrap pseudo-replicates.

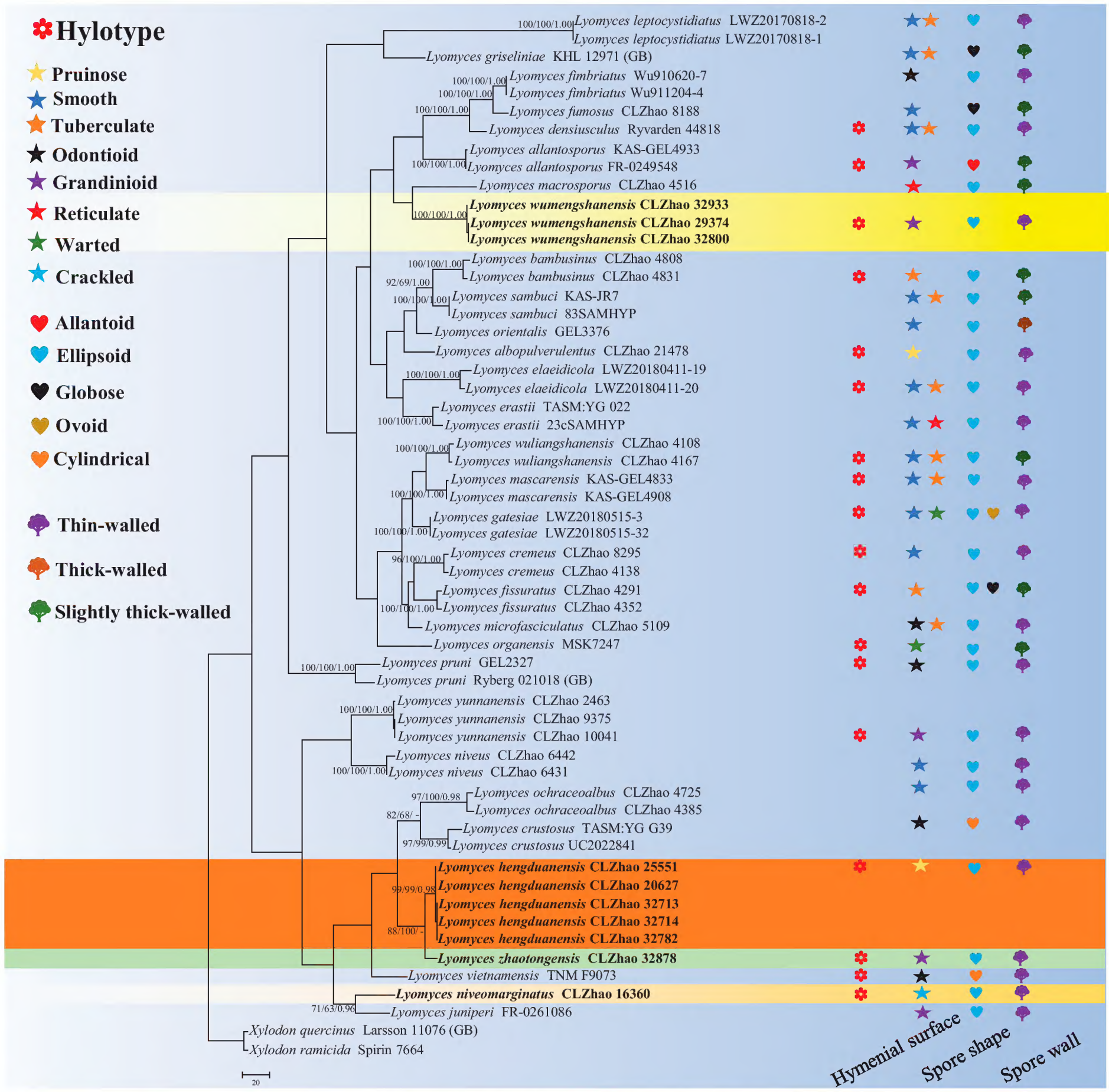

Figure 2. Maximum parsimony strict consensus tree illustrating the phylogeny of the four new species and related species in *Lyomyces*, based on ITS sequences. Branches are labelled with Maximum Likelihood bootstrap values > 70%, parsimony bootstrap values > 50% and Bayesian posterior probabilities > 0.95, respectively.

MrModelTest 2.3 (Nylander 2004) was used to determine the best-fit evolution model for each dataset for Bayesian Inference (BI), which was performed using MrBayes 3.2.7a with a GTR+I+G model of DNA substitution and a gamma distribution rate variation across sites (Ronquist et al. 2012). A total of four Markov chains were run for two runs from random starting trees for 1.905 million generations for ITS+nLSU (Fig. 1) and 2 million generations for ITS (Fig. 2), with trees and parameters sampled every 1,000 generations. The first quarter of all of the generations were discarded as burn-in. A majority rule consensus tree was computed from the remaining trees. Branches were considered as significantly supported if they received a Maximum Likelihood bootstrap support value (BS) of ≥ 70%, a Maximum Parsimony bootstrap support value (BT) of ≥ 70% or a Bayesian Posterior Probability (BPP) of ≥ 0.95.

Results

Molecular phylogeny

The ITS+nLSU dataset (Fig. 1) comprised sequences from 40 fungal specimens representing 29 taxa. The dataset had an aligned length of 2,112 characters, of which 1,298 characters were constant, 254 were variable and parsimony-uninformative and 560 were parsimony-informative. Maximum parsimony analysis yielded one equally parsimonious tree (TL = 2,513, CI = 0.4990, HI = 0.5010, RI = 0.6658 and RC = 0.3322). The best model of nucleotide evolution for the ITS+nLSU dataset estimated and applied in the Bayesian analysis was found to be GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as in the MP analysis. The Bayesian analysis had an average standard deviation of split frequencies = 0.009992 (BI) and the effective sample size (ESS) across the two runs is double the average ESS (avg. ESS) = 2078.5. The phylogram, based on the ITS+nLSU rDNA gene regions (Fig. 1), included three genera within Schizoporaceae (Hymenochaetales), which were *Fasciodontia*, *Lyomyces* and *Xylodon*, in which four new species were grouped into the genera *Lyomyces*.

The ITS dataset (Fig. 2) comprised sequences from 57 fungal specimens representing 33 taxa. The dataset had an aligned length of 696 characters, of which 270 characters were constant, 41 were variable and parsimony-uninformative and 385 were parsimony-informative. Maximum parsimony analysis yielded 80 equally parsimonious tree (TL = 1,748, CI = 0.4027, HI = 0.5973, RI = 0.6935 and RC = 0.2793). The best model of nucleotide evolution for the ITS dataset estimated and applied in the Bayesian analysis was found to be GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as in the MP analysis. The Bayesian analysis had an average standard deviation of split frequencies = 0.014964 (BI) and the effective sample size (ESS) across the two runs is double the average ESS (avg. ESS) = 1,387.5. The phylogenetic tree (Fig. 2), inferred from the ITS sequences, highlighted that *L. hengduanensis* group with *L. zhaotongensis*; and then closely grouped with *L. crustosus* (Pers.) P. Karst., *L. ochraceoalbus* C.L. Zhao and *L. vietnamensis* (Yurchenko & Sheng H. Wu) Riebesehl & Langer. *Lyomyces niveomarginatus* was retrieved as a sister to *L. juniperi* (Bourdot & Galzin) Riebesehl & Langer. *Lyomyces wumengshanensis* was retrieved as a sister to *L. macrosporus* C.L. Zhao. Moreover, *Lyomyces zhaotongensis* grouped with *L. hengduanensis* and closely clustered with *L. crustosus*, *L. ochraceoalbus* and *L. vietnamensis*.

Taxonomy

***Lyomyces hengduanensis* Q. Yuan & C.L. Zhao, sp. nov.**

MycoBank No: 853724

Figs 3, 4

Type material. *Holotype*. CHINA • Yunnan Province, Lincang, Fengqing County, Yaojie Town, GPS coordinates 24°66'N, 100°19'E, altitude 2060 m, on a fallen branch of angiosperm, leg. C.L. Zhao, 22 October 2022, CLZhao 25551 (SWFC).

Etymology. *Hengduanensis* (Lat.) refers to the type locality "Hengduan Mountain".

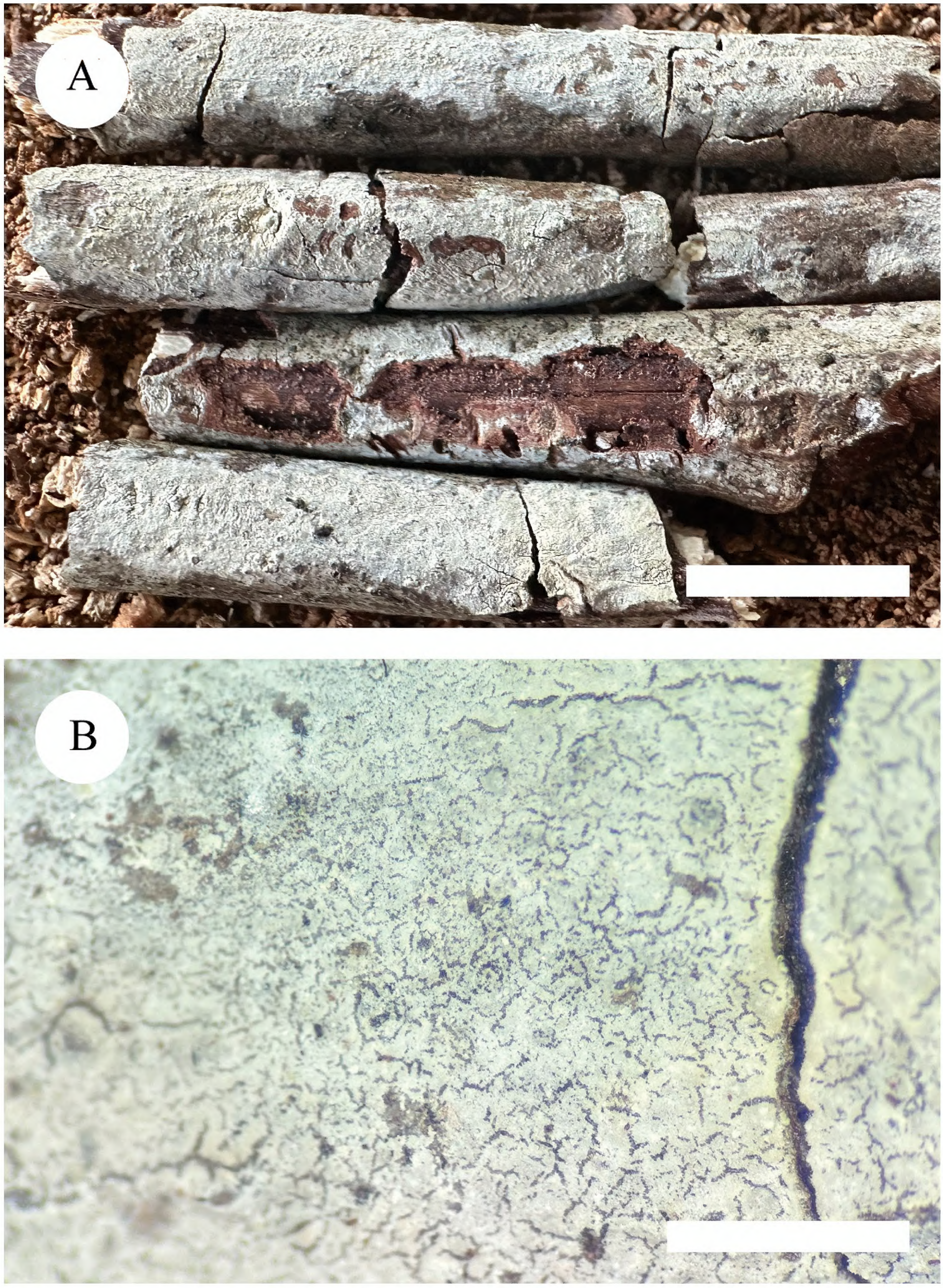

Figure 3. Basidiomata of *Lyomyces hengduanensis* (holotype). Scale bars: 1 cm (**A**); 2 mm (**B**).

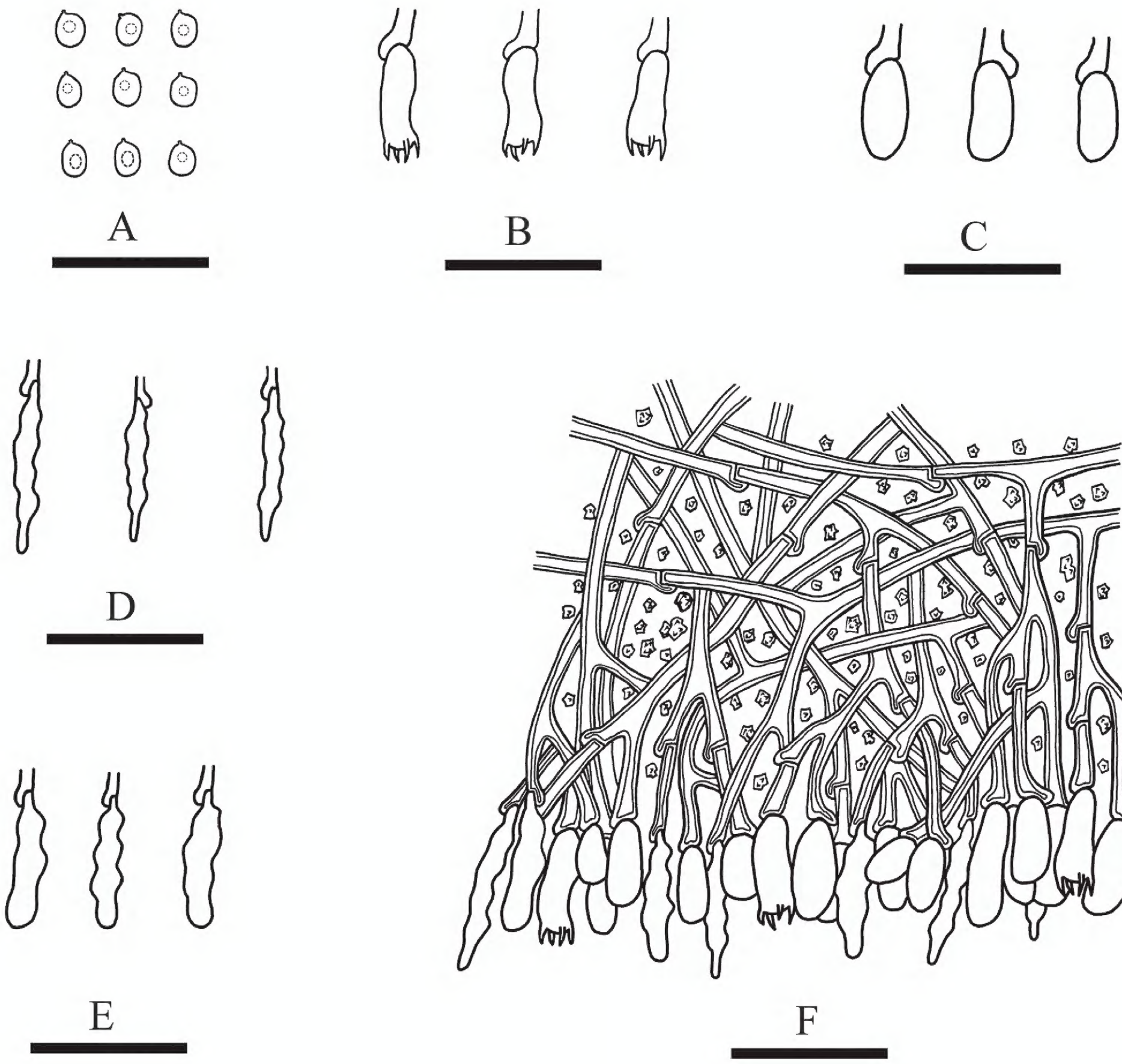

Figure 4. Microscopic structures of *Lyomyces hengduanensis* (holotype): basidiospores (**A**), basidia (**B**), basidioles (**C**), fusoid cystidia (**D**), subclavate cystidia (**E**), a section of hymenium (**F**). Scale bars: 20 μm (**A–F**).

Description. Basidiomata annual, resupinate, adnate, brittle, without odour and taste when fresh and up to 3.5 cm long, 1 cm wide, 100 μm thick. Hymenial surface pruinose, white to cream when fresh, to cream to slightly buff upon drying. Sterile margin white to cream and up to 1 mm wide.

Hyphal system monomitic, generative hyphae with clamp connections, colourless, thick-walled, branched, 2–3 μm in diameter; IKI–, CB–, tissues unchanged in KOH. Numerous crystals present amongst generative hyphae.

Cystidia of two types: (1) fusoid, colourless, thin-walled, smooth, slightly constricted in the middle to somewhat sinuous, 17.5–25 × 3–4 μm; (2) subclavate, colourless, thin-walled, smooth, slightly constricted in the middle to somewhat sinuous, 16–23 × 3–4.5 μm; basidia clavate, with 4 sterigmata and a basal clamp connection, 10.5–14 × 3.5–5 μm.

Basidiospores ellipsoid, colourless, thin-walled, smooth, with one oil drop, CB–, IKI–, 3.5–6 × 3–4.5 µm, L = 4.63 µm, W = 3.65 µm, Q = 1.25–1.28 (n = 90/3).

Additional specimens examined (*paratypes*). CHINA • Yunnan Province, Zhaotong, Qiaojia County, Yaoshan Town, Yaoshan National Nature Reserve, 26°50'N, 102°59'E, altitude 2500 m, on a fallen branch of angiosperm, leg. C.L. Zhao, 22 August 2020, CLZhao 20627 (SWFC) • Zhaotong, Wumeng Mountain National Nature Reserve, GPS coordinates 27°72'N, 103°92'E, altitude 1424 m, on a fallen branch of angiosperm, leg. C.L. Zhao, 29 August 2023, CLZhao 32713, CLZhao 32714, CLZhao 32782 (SWFC).

Lyomyces niveomarginatus Q. Yuan & C.L. Zhao, sp. nov.

MycoBank No: 853725

Figs 5, 6

Type material. *Holotype*. CHINA • Yunnan Province, Wenshan, Wenshan National Nature Reserve, GPS coordinates 23°21'N, 104°10'E, altitude 1950 m, on a fallen branch of angiosperm, leg. C.L. Zhao, 26 July 2019, CLZhao 16360 (SWFC).

Etymology. *Niveomarginatus* (Lat.) refers to the niveous margin of basidiomata.

Description. Basidiomata annual, resupinate, adnate, subceraceous, without odour and taste when fresh and up to 7.5 cm long, 2 cm wide, 150 µm thick. Hymenial surface crackled, white to cream when fresh, to cream to slightly buff upon drying. Sterile margin distinct, whitish and up to 2 mm wide.

Hyphal system monomitic, generative hyphae with clamp connections, colourless, thin-walled, branched, 1.5–3.5 µm in diameter; IKI–, CB–, tissues unchanged in KOH. Numerous crystals present amongst generative hyphae.

Cystidia of two types: (1) fusoid, colourless, thin-walled, smooth, 25–29 × 2–3 µm; (2) clavate, colourless, thin-walled, smooth, 20–25.5 × 4.5–5.5 µm; basidia subclavate, with 4 sterigmata and a basal clamp connection, 23–29 × 2.5–3.5 µm.

Basidiospores ellipsoid, colourless, thin-walled, smooth, with one oil drop, CB–, IKI–, 4.5–7 × (2.5–)3–4 µm, L = 5.51 µm, W = 3.15 µm, Q = 1.75 (n = 30/1).

Additional specimens examined (*paratypes*). CHINA • Yunnan Province, Wenshan, Wenshan National Nature Reserve, GPS coordinates 23°21'N, 104°10'E, altitude 1950 m, on a fallen branch of angiosperm, leg. C.L. Zhao, 7 August 2024, CLZhao 40333, CLZhao 40334 (SWFC).

Lyomyces wumengshanensis Q. Yuan & C.L. Zhao, sp. nov.

MycoBank No: 853726

Figs 7, 8

Type material. *Holotype*. CHINA • Yunnan Province, Zhaotong, Daguan County, Wumeng Mountain National Nature Reserve, GPS coordinates 27°72'N, 103°92'E, altitude 1424 m, on a fallen branch of angiosperm, leg. C.L. Zhao, 3 July 2023, CLZhao 29374 (SWFC).

Etymology. *Wumengshanensis* (Lat.) refers to the type locality "Wumeng Mountain".

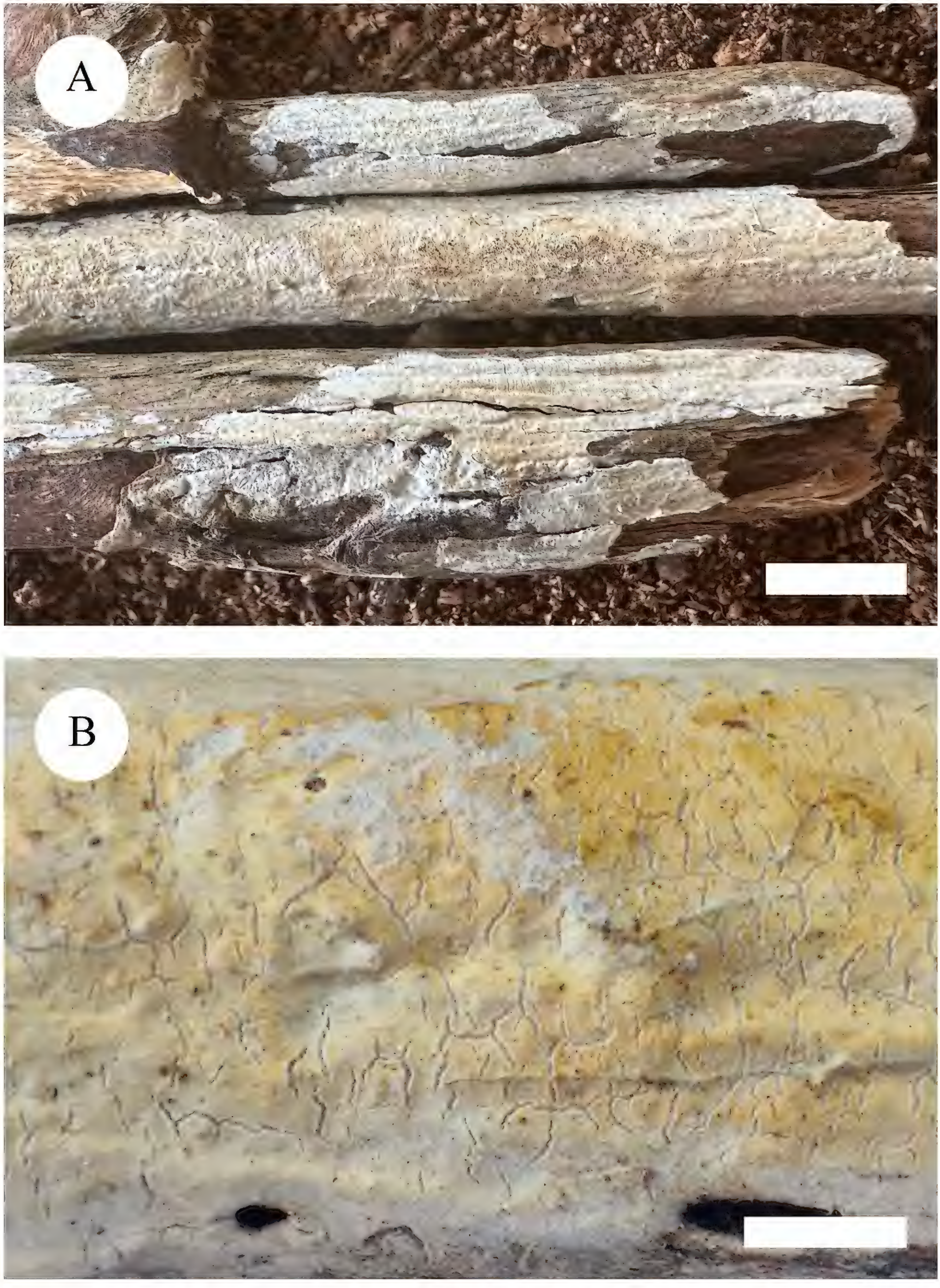

Figure 5. Basidiomata of *Lyomyces niveomarginatus* (holotype). Scale bars: 1 cm (**A**); 2 mm (**B**).

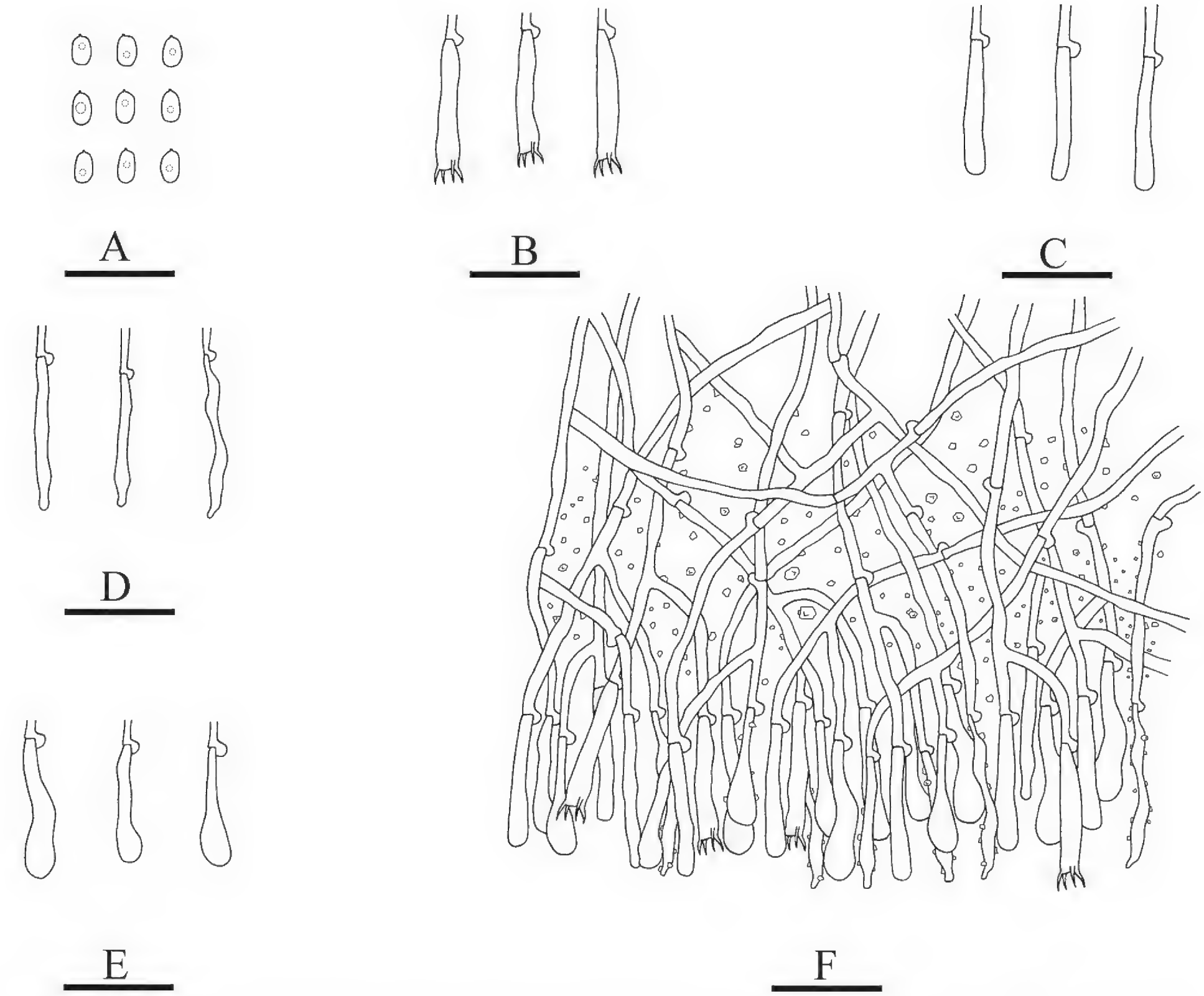

Figure 6. Microscopic structures of *Lyomyces niveomarginatus* (holotype): basidiospores (**A**), basidia (**B**), basidioles (**C**), fusoid cystidia (**D**), clavate cystidia (**E**), a section of hymenium (**F**). Scale bars: 20 μm (**A–F**).

Description. Basidiomata annual, resupinate, adnate, coriaceous when fresh, becoming farinaceous upon drying, without odour and taste when fresh and up to 5 cm long, 2 cm wide, 150 μm thick. Hymenial surface grandinioid, white when fresh, to cream upon drying. Sterile margin white and up to 1 mm wide.

Hyphal system monomitic, generative hyphae with clamp connections, colourless, thick-walled, branched, 3–4 μm in diameter; IKI–, CB–, tissues unchanged in KOH. Numerous crystals present amongst generative hyphae.

Cystidia capitate, colourless, thin-walled, smooth, 24.5–29 × 3–4 μm; basidia subclavate to barrelled, colourless, with 4 sterigmata and a basal clamp connection, 11.5–14 × 5.5–6.5 μm.

Basidiospores ellipsoid to broad ellipsoid, colourless, thin-walled, smooth, with one oil drop, CB–, IKI–, 4–6 × 3–5 μm, L = 5.4 μm, W = 4.2 μm, Q = 1.28–1.32 (n = 120/4).

Additional specimen examined (*paratype*). China • Yunnan Province, Zhaotong, Wumeng Mountain National Nature Reserve, 27°72'N, 103°92'E, altitude 1424 m, on a fallen branch of angiosperm, leg. C.L. Zhao, 29 August 2023, CLZ-

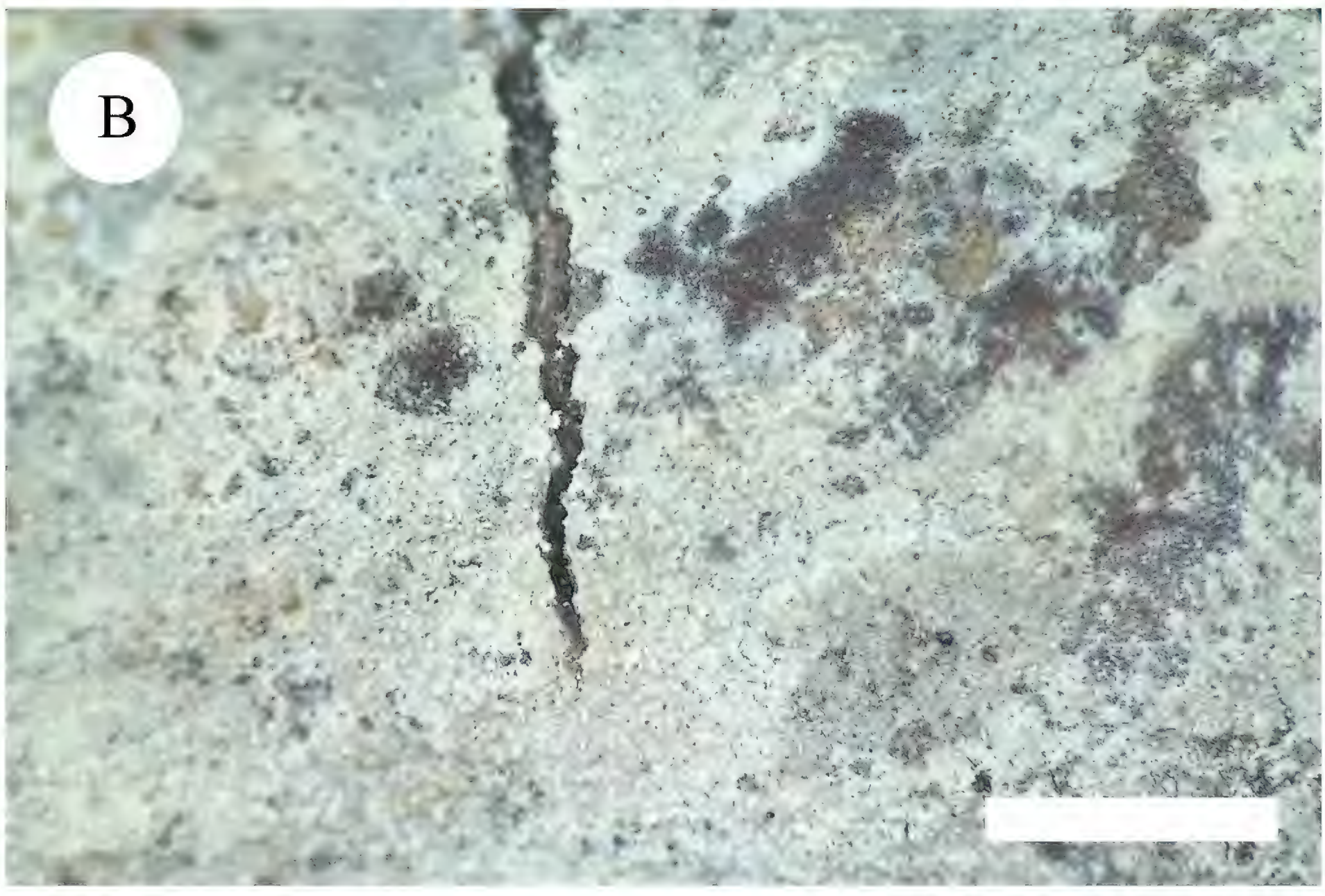

Figure 7. Basidiomata of *Lyomyces wumengshanensis* (holotype). Scale bars: 1 cm (**A**); 2 mm (**B**).

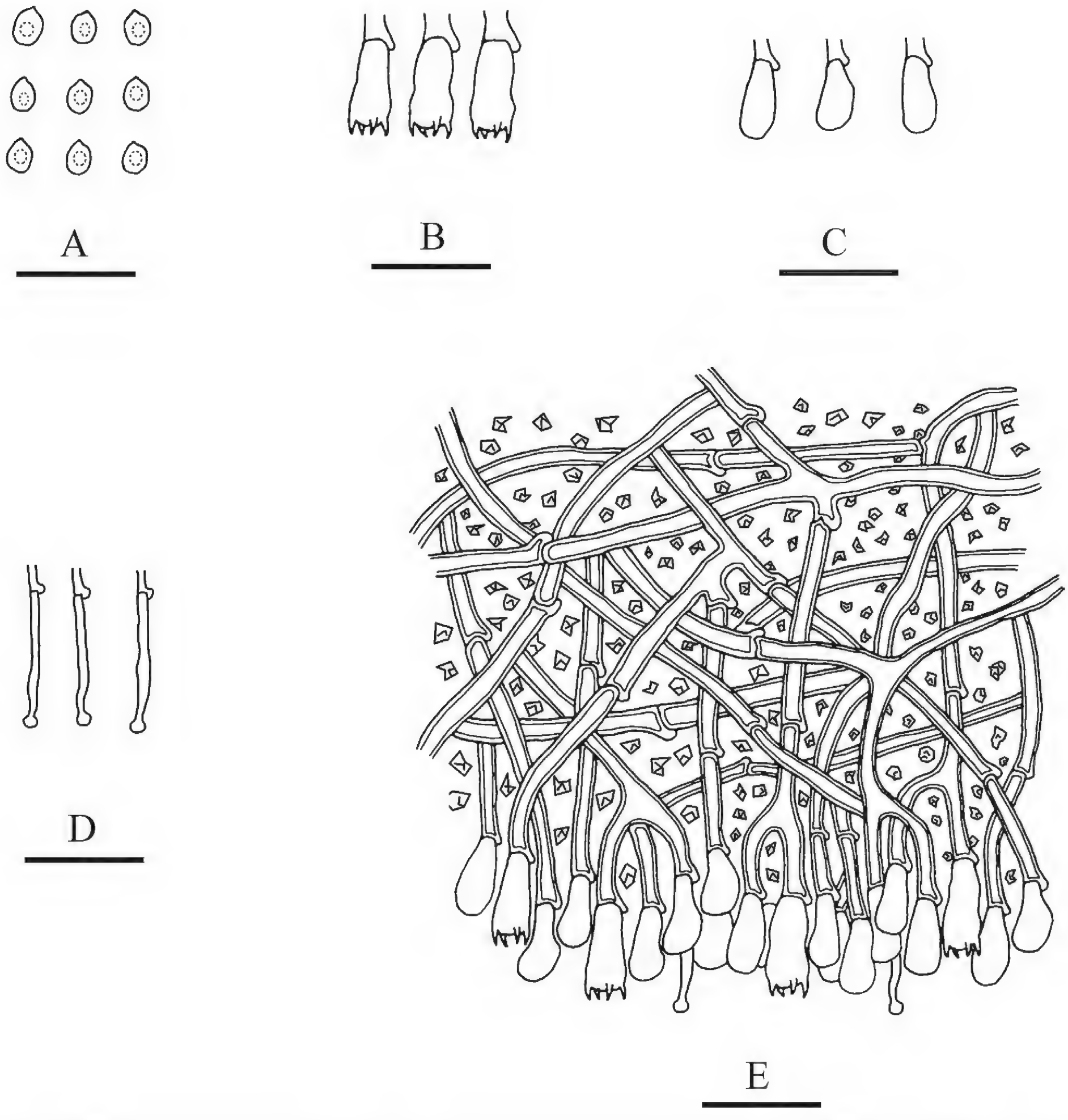

Figure 8. Microscopic structures of *Lyomyces wumengshanensis* (holotype): basidiospores (**A**), basidia (**B**), basidioles (**C**), capitate cystidia (**D**), a section of hymenium (**E**). Scale bars: 10 μm (**A–E**).

hao 31486, CLZhao 32705, CLZhao 32736, CLZhao 32800, CLZhao 32869, CLZhao 32915, CLZhao 32933 (SWFC).

***Lyomyces zhaotongensis* Q. Yuan & C.L. Zhao, sp. nov.**

MycoBank No: 853727

Figs 9, 10

Type material. *Holotype*. CHINA •Yunnan Province, Zhaotong, Wumeng Mountain National Nature Reserve, GPS coordinates 27°77'N, 104°29'E, altitude

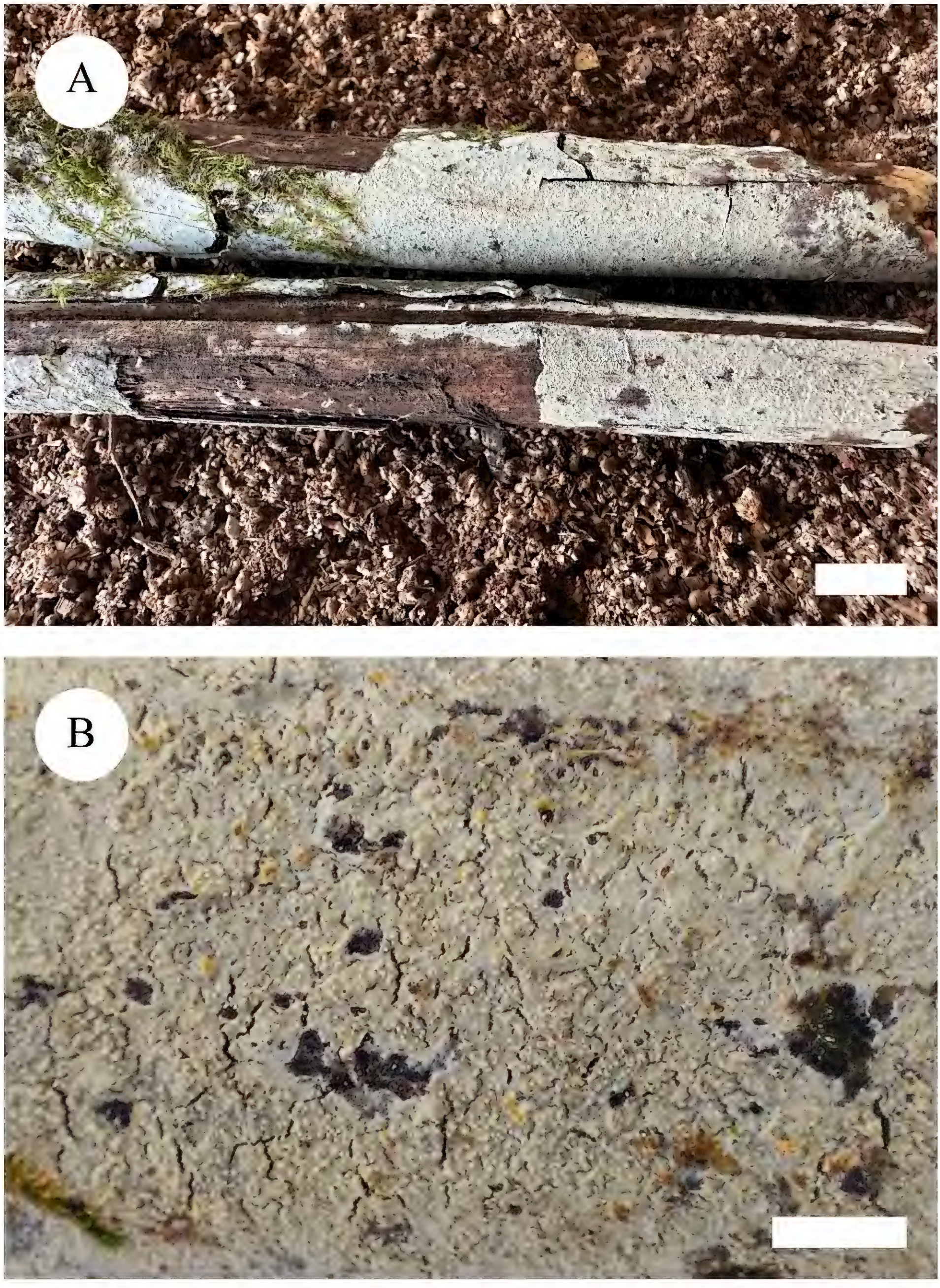

Figure 9. Basidiomata of *Lyomyces zhaotongensis* (holotype). Scale bars: (**A**) 1 cm; (**B**) 2 mm.

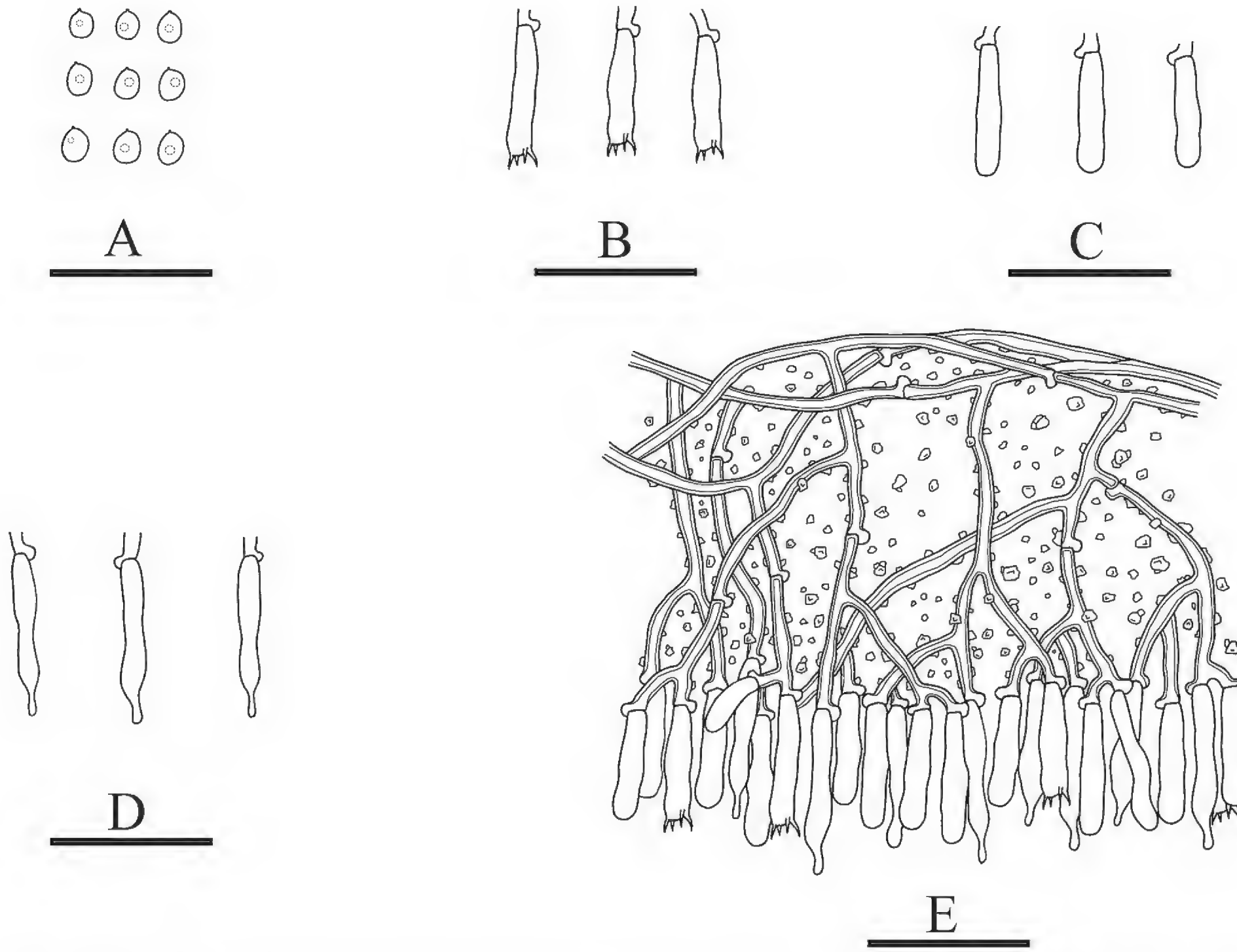

Figure 10. Microscopic structures of *Lyomyces zhaotongensis* (holotype): basidiospores (**A**), basidia (**B**), basidioles (**C**), fusoid cystidia (**D**), a section of hymenium (**E**). Scale bars: 20 μm (**A–E**).

2900 m, on the fallen branch of angiosperm, leg. C.L. Zhao, 29 August 2023, CLZhao 32878 (SWFC).

Etymology. *Zhaotongensis* (Lat.) refers to the type locality "Zhaotong".

Description. Basidiomata annual, resupinate, adnate, farinaceous when fresh, becoming coriaceous upon drying and up to 9.5 cm long, 3 cm wide, 30–80 um thick. Hymenial surface grandinioid, cream when fresh and cream to buff upon drying. Sterile margin white to cream and up to 1 mm wide.

Hyphal system monomitic, generative hyphae with clamp connections, colourless, thick-walled, branched, 1.5–2 μm in diameter; IKI–, CB–, tissues unchanged in KOH. Numerous crystals present amongst generative hyphae.

Cystidia fusoid, colourless, thin-walled, smooth, 16–20.5 × 2.5–3.5 μm. Basidia clavate, with 4 sterigmata and a basal clamp connection, 14–16.5 × 2.5–3.5 μm.

Basidiospores broadly ellipsoid, colourless, thin-walled, smooth, with oil drops, CB–, IKI–, 2.6–3.5 × 2.5–3 μm, L = 2.99 μm, W = 2.75 μm, Q = 1.08 (n = 30/1).

Additional specimen examined (*paratype*). CHINA • Yunnan Province, Zhaotong, Wumeng Mountain National Nature Reserve, GPS coordinates 27°77'N, 104°29'E, altitude 2900 m, on the fallen branch of angiosperm, leg. C.L. Zhao, 10 August 2024, CLZhao 40335 (SWFC).

Discussion

Many recently new wood-inhabiting fungal taxa have been reported in the subtropics and tropics, including in the genus *Lyomyces* (Xiong et al. 2009; Chen et al. 2017; Kan et al. 2017a, b; Riebesehl and Langer 2017; Viner et al. 2018; Chen and Zhao 2020; Luo et al. 2021a, b, c, 2022; Qu and Zhao 2022; Qu et al. 2022; Viner et al. 2022; Guan et al. 2023; Deng et al. 2024a, b; Zhang et al. 2024). Prior to this study, the following sixteen *Lyomyces* species were reported from China as *L. albopulverulentus* C.L. Zhao, *L. albus* (Sheng H. Wu) Riebesehl & Langer, *L. bambusinus*, *L. capitatocystidiatus* (H.X. Xiong, Y.C. Dai & Sheng H. Wu) Riebesehl & Langer, *L. cremeus* C.L. Zhao, *L. fissuratus*, *L. fumosus*, *L. leptocystidiatus* Xue W. Wang & L.W. Zhou, *L. macrosporus* C.L. Zhao & K.Y. Luo, *L. microfasciculatus* (Yurchenko & Sheng H. Wu) Riebesehl & Langer, *L. niveus*, *L. ochraceoalbus*, *L. sambuci*, *L. tenuissimus* (Yurchenko & Sheng H. Wu) Riebesehl & Langer, *L. wuliangshanensis* C.L. Zhao and *L. yunnanensis* C.L. Zhao (Xiong et al. 2009; Yurchenko et al. 2013; Riebesehl and Langer 2017; Chen and Zhao 2020; Luo et al. 2021b, c; Wang et al. 2021). The present study reports four new species in the genus *Lyomyces*, based on a combination of morphological features and molecular evidence.

Phylogenetically, based on the multiple loci in *Hyphodontia* s.l., six genera of *Fasciodontia*, *Hastodontia*, *Hyphodontia*, *Lyomyces*, *Kneiffiella* and *Xylodon*, were divided into four clades in the wood-inhabiting fungal order Hymenochaetales (Wang et al. 2021). In the present study, the phylogram inferred from the ITS+nLSU data, four new species grouped into the genus *Lyomyces* (Fig. 1). Based on ITS topology (Fig. 2), in which *L. hengduanensis* group with *L. zhaotongensis* and then closely grouped with *L. crustosus*, *L. ochraceoalbus* and *L. vietnamensis*. *Lyomyces niveomarginatus* was retrieved as a sister to *L. juniperi*. *L. wumengshanensis* was sister to *L. macrosporus*. Moreover, *L. zhaotongensis* grouped with *L. hengduanensis* and then closely clustered with three species: *L. crustosus*, *L. ochraceoalbus* and *L. vietnamensis*. However, morphologically, *L. zhaotongensis* can be delimited from *L. hengduanensis* by its the grandinioid hymenial surface and longer basidia (14–16.5 × 2.5–3.5 µm); *L. crustosus* can be separated from *L. hengduanensis* by its odontioid hymenial surface and narrow basidiospores (5–7.5 × 2.5–3 µm) (Lentz and McKay 1976); *L. ochraceoalbus* differs in *L. hengduanensis* by having a smooth hymenial surface and lacking a cystidium (Luo et al. 2021c); *L. vietnamensis* differs from *L. hengduanensis* by its aculeate hymenial surface and narrow basidiospores (5.8–6.1 × 2.6–2.9 µm; Yurchenko and Wu (2013)). *L. juniperi* can be delimited from *L. niveomarginatus* by its smooth hymenial surface with some scattered small granules and wider basidia (15–25 × 4–4.5 µm; Hjortstam and Ryvarden (2004)); *L. macrosporus* can be separated from *L. wumengshanensis* by its reticulate hymenial surface and longer basidiospores (6.7–8.9 × 4.4–5.4 µm; Chen and Zhao (2020)); *L. crustosus* can be delimited from *L. zhaotongensis* by its odontioid hymenial surface and longer basidiospores (5–7.5 × 2.5–3 µm; Lentz and McKay (1976)); *L. hengduanensis* can be delimited from *L. zhaotongensis* by its pruinose hymenial surface and shorter basidia (14–16.5 × 2.5–3.5 µm); *L. ochraceoalbus* differs in *L. zhaotongensis* by having smooth hymenial surface and longer basidiospores (4–5 × 2.5–3.5 µm; Luo et al. (2021c)); *L. vietnamensis* can be delimited from *L. zhaotongensis* by its

aculeate hymenial surface and longer basidiospores (5.8–6.1 × 2.6–2.9 µm; Yurchenko and Wu (2013)).

Morphologically, *Lyomyces hengduanensis* resembles four taxa viz. *L. albopulverulentus*, *L. bambusinus*, *L. mascarensis* Riebesehl, Yurch. & Langer and *L. yunnanensis*, by the similar ellipsoid basidiospores. However, *L. albopulverulentus* differs from *L. hengduanensis* by its larger basidia (24.5–28.5 × 7–9 µm) and basidiospores (8–10.5 × 5.5–7 µm; Guan et al. (2023)); *L. bambusinus* can be separated from *L. hengduanensis* by its colliculose to tuberculate hymenial surface and longer basidia (16.5–35 × 3.5–7 µm; Chen and Zhao (2020)); *L. mascarensis* is distinct from *L. hengduanensis* by having indistinctly colliculose hymenial surface and longer basidia (16–17.5 × 3.5–4.5 µm; Yurchenko et al. (2017)); *L. yunnanensis* is distinguished from *L. hengduanensis* by its grandinioid hymenial surface and longer basidia (16.5–27 × 4–5.5 µm; Guan et al. (2023)).

Morphologically, *Lyomyces niveomarginatus* resembles several species viz. *L. albopulverulentus*, *L. cremeus*, *L. macrosporus*, *L. wuliangshanensis* and *L. yunnanensis* by the cream to buff hymenial surface and ellipsoid basidiospores. However, *L. albopulverulentus* differs from *L. niveomarginatus* by its pruinose hymenial surface and wider basidia (24.5–28.5 × 7–9 µm; Guan et al. (2023)); *L. cremeus* can be separated from *L. niveomarginatus* by its smooth hymenial surface and shorter basidia (9–18.5 × 3–6 µm; Chen and Zhao (2020)); *L. macrosporus* differs from *L. niveomarginatus* by its reticulate hymenial surface and wider basidia (23–29 × 2.5–3.5 µm) and wider basidiospores (6.7–8.9 × 4.4–5.4 µm; Chen and Zhao (2020)); *L. wuliangshanensis* can be delimited from *L. niveomarginatus* by its smooth to more or less tuberculate hymenial surface and shorter basidia (12–20 × 3–4.3 µm; Chen and Zhao (2020)); *L. yunnanensis* is distinct from *L. niveomarginatus* by having grandinioid hymenial surface and wider basidia (16.5–27 × 4–5.5 µm; Guan et al. (2023)).

Morphologically, *Lyomyces wumengshanensis* resembles *L. bambusinus*, *L. cremeus*, *L. fumosus*, *L. fissuratus*, *L. wuliangshanensis* and *L. yunnanensis* by having the capitate cystidia. However, *L. bambusinus* is distinct from *L. wumengshanensis* by possessing tapering cystidia (40–65 × 4–5.5 µm) and longer basidia (16.5–35 × 3.5–7 µm; Chen and Zhao (2020)); *L. cremeus* differs from *L. wumengshanensis* by its smooth hymenial surface and possesses tapering cystidia (18–35 × 3–4.5 µm; Chen and Zhao (2020)); *L. fumosus* can be separated from *L. wumengshanensis* by its smooth, smoky grey hymenial surface and narrower basidia (11.5–17.5 × 3–5 µm; Luo et al. (2021b)); *L. fissuratus* can be delimited from *L. wumengshanensis* by its longer and narrower basidia (14.7–23.3 × 2.9–4.8 µm; Luo et al. (2021b)); *L. wuliangshanensis* differs from *L. wumengshanensis* by its smooth to more or less tuberculate hymenial surface and narrower basidia (12–20 × 3–4.3 µm; Chen and Zhao (2020)); *L. yunnanensis* is separated from *L. wumengshanensis* by the longer basidia (16.5–27 × 4–5.5 µm) and possessing fusiform cystidia (18–39 × 4–6 µm; Guan et al. (2023)).

Morphologically, *Lyomyces zhaotongensis* reminds *L. albopulverulentus*, *L. cremeus*, *L. denudatus* Viner, *L. macrosporus* and *L. wuliangshanensis* by having the ellipsoid basidiospores. However, *L. albopulverulentus* can be separated from *L. zhaotongensis* by its pruinose hymenial surface and larger basidia (24.5–28.5 × 7–9 µm) and larger basidiospores (8–10.5 × 5.5–7 µm; Guan et al. (2023)); *L. cremeus* is distinct from *L. zhaotongensis* by its smooth hymenial surface and larger basidiospores (4.5–5.6 × 3.3–4.3 µm; Chen and Zhao

(2020)); *L. denudatus* is separated from *L. zhaotongensis* by the smooth hymenial surface and longer basidiospores (4.8–7 × 2.8–4.2 µm; Viner and Miettinen (2022)); *L. macrosporus* differs from *L. zhaotongensis* due to its reticulate hymenial surface and larger basidia (22.2–38 × 4.5–7 µm) and larger basidiospores (6.7–8.9 × 4.4–5.4 µm; Chen and Zhao (2020)); *L. wuliangshanensis* can be delimited from *L. zhaotongensis* by its smooth to more or less tuberculate hymenial surface and longer basidiospores (3.5–5.3 × 2.8–4 µm; Chen and Zhao (2020)). A morphological comparison amongst four new *Lyomyces* species and seven similar species are presented in Table 2.

The Basidiomycota is a major phylum of the kingdom Fungi (He et al. 2019; Wijayawardene et al. 2020; Yuan et al. 2023; He et al. 2024), in which the wood-inhabiting fungi are an extensively studied group of Basidiomycota (Gilbertson and Ryvarden 1987; Bernicchia and Gorjón 2010; Núñez and Ryvarden 2001; Dai 2012; Ryvarden and Melo 2014; Wu et al. 2022b; Zhao et al. 2023; Dong et al. 2024), but the wood-inhabiting fungal diversity is still not well known in China, especially in subtropical and tropical areas, and many recently-described taxa of this ecologically important group were from China (Zhao et al. 2014; Zhao et al. 2015; Zhao et al. 2016; Bian et al. 2016; Ma and Zhao 2019; Guan et al. 2020; Huang and Zhao 2020; Guan et al. 2023; Ji et al. 2023; Liu et

Table 2. A morphological comparison between four new *Lyomyces* species and seven similar species in the genus *Lyomyces*. The bold are new taxa.

Species name	Hymenial surface	Generative hyphae	Cystidia	Basidia	Basidiospores	References
Lyomyces albopulverulentus	Pruinose/ white	Thick-walled/ frequently branched	Capitate, 37–54 × 5–9 µm	Clavate, 24.5–28.5 × 7–9 µm	Ellipsoid, (7.5–)8–10.5(–11) × (5–)5.5–7 µm	Guan et al. (2023)
Lyomyces bambusinus	Colliculose to tuberculate/ cream to buff	Thick-walled/ branched	Capitate, 35–55 × 4–7 µm; tapering, 40–65 × 4–5.5 µm, cystidioles, 12–17 × 2–3 µm	Clavate, 16.5–35 × 3.5–7 µm	Broadly ellipsoid, (4.5–)4.7–5.9 (–6.2) × (3.4–)3.7–4.6(–4.8) µm	Chen and Zhao (2020)
Lyomyces cremeus	Smooth/ pale cream	Thick-walled/ branched	Capitate, 20–40 × 3–5 µm; tapering, 18–35 × 3–4.5 µm	Clavate, 9–18.5 × 3–6 µm	Ellipsoid, 4.5–5.6(–5.8) × 3.3–4.3(–4.5) µm	Chen and Zhao (2020)
Lyomyces denudatus	Smooth/ cream	Thin-walled to slightly thick-walled	Capitate, (21–)34.9–62 × (3.5–)4–5.5(–7) µm	Suburniform, 15–21.1(–25) × 3.8–5.5 µm	Ellipsoid, (4.1–)4.8–7 × 2.8–4.2(–4.7) µm	Viner and Miettinen (2022)
Lyomyces hengduanensis	Pruinose/ cream to slightly buff	Thick-walled/ branched	Fusoid, 17.5–25 × 3–4 µm; subclavate, 16–23 × 3–4.5 µm	Clavate, 10.5–14 × 3.5–5 µm	Ellipsoid, 3.5–6 × 3–4.5 µm	**Present study**
Lyomyces mascarensis	Smooth / cream or brownish	Thin-walled	Capitate, 17–38 × 3.5–6(–7) µm; submoniliform, 18–22 × 5–5.5 µm; tapering, 25–30 × 3.5–4.5 µm	Subcylindrical with one constriction, 16–17.5(–19) × 3.5–4.5(–6) µm	Ellipsoid or broadly ellipsoid, (4–)4.5–6 × (3–)3.3–4 µm	Yurchenko et al. (2017)
Lyomyces niveomarginatus	Smooth / cream to slightly buff	Thin-walled, branched	Fusoid, 25–29 × 2–3 µm; clavate, 20–25.5 × 4.5–5.5 µm	Subclavate, 23–29 × 2.5–3.5 µm	Ellipsoid, 4.5–7 × (2.5–)3–4 µm	**Present study**
Lyomyces wuliangshanensis	Tuberculate/ cream to buff	Thick-walled/ branched	Capitate, 22–37 × 3–6 µm; tapering, 21–35 × 4–6.5 µm	Clavate, 12–20 × 3–4.3 µm	Ellipsoid, (3.3–)3.5–5.3(–5.5) × 2.8–4(–4.2) µm	Chen and Zhao (2020)
Lyomyces wumengshanensis	Grandinioid/ white to cream	Thick-walled/ branched	Capitate, 24.5–29 × 3–4 µm	Subclavate to barreled, 11.5–14 × 5.5–6.5 µm	Ellipsoid to broad ellipsoid, 4–6 × 3–5 µm	**Present study**
Lyomyces yunnanensis	Grandinioid/ cream to buff	Thick-walled, frequently branched	Tapering, 18–39 × 4–6 µm; capitate, 16–23.5 × 3–5 µm	Clavate, 16.5–27 × 4–5.5 µm	Ellipsoid, (4.5–)5–7 × 3–4.5 µm	Guan et al. (2023)
Lyomyces zhaotongensis	Grandinioid/ cream to buff	Thick-walled/ branched	Fusoid, 16–20.5 × 2.5–3.5 µm	Clavate, 14–16.5 × 2.5–3.5 µm	Broadly ellipsoid, 2.6–3.5 × 2.5–3 µm	**Present study**

al. 2023; Yang et al. 2023; Deng et al. 2024a, b; Yang et al. 2024; Zhang et al. 2024; Zhou et al. 2024). Four new species in the present study are described, based on morphological and molecular phylogenetic analyses, also from the subtropics. This study enriches the wood-inhabiting fungal diversity in China and the world.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

The research was supported by the National Natural Science Foundation of China (Project No. 32170004, U2102220), Forestry Innovation Programs of Southwest Forestry University (Grant No: LXXK-2023Z07), the High-level Talents Program of Yunnan Province (YNQR-QNRC-2018-111).

Author contributions

Conceptualization, C.Z.; methodology, C.Z. and Q.Y.; software, C.Z.; validation, C.Z.and Q.Y.; formal analysis, C.Z. and Q.Y.; investigation, C.Z., Q.Y., Y.D. Y.L., K.W. and Y.W.; resources, C.Z.; writing—original draft preparation, C.Z. and Q.Y.; writing—review and editing, C.Z. and Q.Y.; visualization, C.Z. and Q.Y.; supervision, C.Z.; project administration, C.Z.; funding acquisition, C.Z. All authors have read and agreed to the published version of the manuscript.

Author ORCIDs

Qi Yuan https://orcid.org/0000-0002-6732-1656
Yunchao Li https://orcid.org/0009-0007-3500-3761
Yunfei Dai https://orcid.org/0009-0007-7734-4142
Kunyan Wang https://orcid.org/0009-0004-1678-9963
Changlin Zhao https://orcid.org/0000-0002-8668-1075

Data availability

All of the data that support the findings of this study are available in the main text.

References

Bernicchia A, Gorjón SP (2010) Fungi Europaei 12: Corticiaceae s.l. Edizioni Candusso, Alassio, Italy, 1008 pp.

Bian LS, Wu F, Dai YC (2016) Two new species of *Coltricia* (Hymenochaetaceae, Basidiomycota) from Southern China based on evidence from morphology and DNA sequence data. Mycological Progress 15: 27. https://doi.org/10.1007/s11557-016-1173-0

Chen JZ, Zhao CL (2020) Morphological and molecular identification of four new resupinate species of *Lyomyces* (Hymenochaetales) from southern China. Mycokeys 65: 101–118. https://doi.org/10.3897/mycokeys.65.48660

Chen CC, Wu SH, Chen CY (2017) Three new species of *Hyphodontia* s.l. (Basidiomycota) with poroid or raduloid hymenophore. Mycological Progress 16(5): 553–564. https://doi.org/10.1007/s11557-017-1286-0

Cui BK, Li HJ, Ji X, Zhou JL, Song J, Si J, Yang ZL, Dai YC (2019) Species diversity, taxonomy and phylogeny of Polyporaceae (Basidiomycota) in China. Fungal Diversity 97(1): 137–392. https://doi.org/10.1007/s13225-019-00427-4

Cunningham GH (1959) Hydnaceae of New Zealand. Part II. The genus *Odontia*. Transactions of the Royal Society of New Zealand 86: 65–103.

Cunningham GH (1963) The Thelephoraceae of Australia and New Zealand. Bulletin of the New Zealand Department of Scientific and Industrial Research 145: 1–359.

Dai YC (2010) Hymenochaetaceae (Basidiomycota) in China. Fungal Diversity 45(1): 131–343. https://doi.org/10.1007/s13225-010-0066-9

Dai YC (2011) A revised checklist of corticioid and hydnoid fungi in China for 2010. Mycoscience 52(1): 69–79. https://doi.org/10.1007/S10267-010-0068-1

Dai YC (2012) Polypore diversity in China with an annotated checklist of Chinese polypores. Mycoscience 53(1): 49–80. https://doi.org/10.1007/s10267-011-0134-3

Deng YL, Jabeen SN, Zhao CL (2024a) Species diversity and taxonomy of *Vararia* (Russulales, Basidiomycota) with descriptions of six species from Southwestern China. MycoKeys 103: 97–128. https://doi.org/10.3897/mycokeys.103.118980.

Deng YL, Li JF, Zhao CL, Zhao J (2024b) Four new fungal species in forest ecological system from southwestern China. Journal of Fungi 10: 194. https://doi.org/10.3390/jof10030194

Dong JH, Li Q, Yuan Q, Luo YX, Zhang XC, Dai YF, Zhou Q, Liu XF, Deng YL, Zhou HM, Muhammad A, Zhao CL (2024) Species diversity, taxonomy, molecular systematics and divergence time of wood-inhabiting fungi in Yunnan-Guizhou Plateau, Asia. Mycosphere 15: 1110–1293. https://doi.org/10.5943/mycosphere/15/1/10

Felsenstein J (1985) Confidence intervals on phylogenetics: An approach using bootstrap. Evolution. International Journal of Organic Evolution 39(4): 783–791. https://doi.org/10.2307/2408678

Gafforov Y, Riebesehl J, Ordynets A, Langer E, Yarasheva M, Ghobad-Nejhad M, Zhou LW, Wang XW, Gugliotta AM (2017) *Hyphodontia* (Hymenochaetales, Basidiomycota) and similar taxa from Central Asia. Botany 95(11): 1041–1056. https://doi.org/10.1139/cjb-2017-0115

Gilbertson RL, Ryvarden L (1987) North American polypores 1–2. Fungiflora, Oslo, 433 pp.

Guan QX, Zhao TJ, Zhao CL (2020) Morphological characters and phylogenetic analyses reveal two new species of *Peniophorella* from Southern China. Mycological Progress 19: 397–404. https://doi.org/10.1007/s11557-020-01568-6

Guan QX, Huang J, Huang J, Zhao CL (2023) Five new species of Schizoporaceae (Basidiomycota, Hymenochaetales) from East Asia. MycoKeys 96: 25–56. https://doi.org/10.3897/mycokeys.96.99327

He SH, Li HJ (2013) *Pseudochaete latesetosa* and *P. subrigidula* spp. nov. (Hymenochaetales, Basidiomycota) from China based on morphological and molecular characters. Mycological Progress 12(2): 331–339. https://doi.org/10.1007/s11557-012-0838-6

He MQ, Zhao RL, Hyde KD, Begerow D, Kemler M, Yurkov A, McKenzie EHC (2019) Notes, outline and divergence times of Basidiomycota. Fungal Diversity 99: 105–367. https://doi.org/10.1007/s13225-019-00435-4

He MQ, Cao B, Liu F, Boekhout T, Denchev TT, Schoutteten N, Denchev CM, Kemler M, Gorjón SP, Begerow D and Valenzuela R (2024) Phylogenomics, divergence times and notes of orders in Basidiomycota. Fungal diversity 126: 127–406. https://doi.org/10.1007/s13225-024-00535-w

Hjortstam K, Ryvarden L (2004) Some new and noteworthy corticioid fungi (Basidiomycotina, Aphyllophorales) from Japan. Synopsis Fungorum 18: 8–13.

Hjortstam K, Ryvarden L (2009) A checklist of names in *Hyphodontia* sensu stricto-sensu lato and *Schizopora* with new combinations in *Lagarobasidium*, *Lyomyces*, *Kneiffiella*, *Schizopora*, and *Xylodon*. Synopsis Fungorum 26: 33–55.

Hu Y, Karunarathna SC, Li H, Galappaththi MC, Zhao CL, Kakumyan P, Mortimer PE (2022) The impact of drying temperature on basidiospore size. Diversity 14(4): 239. https://doi.org/10.3390/d14040239

Huang RX, Zhao CL (2020) Three new species of *Phlebia* (Polyporales, Basidiomycota) based on the evidence from morphology and DNA sequence data. Mycological Progress 19, 753–767. https://doi.org/10.1007/s11557-020-01591-7

Hyde KD (2022) The numbers of fungi. Fungal Diversity 114(1): 1. https://doi.org/10.1007/s13225-022-00507-y

Ji X, Sun YF, Wu DM, Gao N, Cui BK (2023) An updated phylogenetic assessment and taxonomic revision of *Perenniporia* sensu lato (Polyporales, Basidiomycota). Journal of Fungi 9: 173. https://doi.org/10.3390/jof9020173

Jiang N, Voglmayr H, Bian DR, Piao CG, Wnag SK, Li Y (2021) Morphology and phylogeny of *Gnomoniopsis* (Gnomoniaceae, Diaporthales) from fagaceae leaves in China. Journal of Fungi 7(10): 792. https://doi.org/10.3390/jof7100792

Kan YH, Gafforov Y, Li T, Zhou LW (2017a) *Hyphodontia zhixiangii* sp. nov. (Schizoporaceae, Basidiomycota) from Uzbekistan. Phytotaxa 299(2): 273–279. https://doi.org/10.11646/phytotaxa.299.2.12

Kan YH, Qin WM, Zhou LW (2017b) *Hyphodontia mollissima* sp. nov. (Schizoporaceae, Hymenochaetales) from Hainan, southern China. Mycoscience 58(4): 297–301. https://doi.org/10.1016/j.myc.2017.04.003

Karsten PA (1881) Enumeratio Thelephorearum Fr. et Clavariearum Fr. Fennicarum, systemate novo dispositarum. Revue Mycologique Toulouse 3: 21–23.

Karsten PA (1882) Rysslands, Finlands och den Skandinaviska halföns Hattsvampar. Sednare Delen: Pip-, Tagg-, Hud-, Klubboch Gelésvampar. Bidrag till Kännedom av Finlands Natur och. Folk 37: 1–257.

Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20(4): 1160–1166. https://doi.org/10.1093/bib/bbx108

Langer E (1994) Die Gattung *Hyphodontia* John Eriksson. Bibliotheca Mycologica, Schweizerbart Science Publishers, Stuttgart, Germany, Vol. 154, 298 pp.

Larsson A (2014) AliView: A fast and lightweight alignment viewer and editor for large data sets. Bioinformatics 30(22): 3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Larsson KH, Larsson E, Kõljalg U (2004) High phylogenetic diversity among corticioid homobasidiomycetes. Mycological Research 108(9): 983–1002. https://doi.org/10.1017/S0953756204000851

Larsson KH, Parmasto E, Fischer M, Langer E, Nakasone KK, Redhead SA (2006) Hymenochaetales: A molecular phylogeny for the hymenochaetoid clade. Mycologia, 98: 926–936. https://doi.org/10.1080/15572536.2006.11832622

Lentz PL, McKay HH (1976) Basidiocarp and culture descriptions of *Hyphoderma* and *Hyphodontia* (Corticiaceae) in the Mississippi Delta Region. Memoirs of the New York Botanical Garden 28: 141–162.

Liu S, Shen LL, Xu TM, Song CG, Gao N, Wu DM, Sun YF, Cui BK (2023) Global diversity, molecular phylogeny and divergence times of the brown-rot fungi within the Polyporales. Mycosphere 14: 1564–1664. https://doi.org/10.5943/mycosphere/14/1/18

Luo KY, Zhao CL (2021) *Fasciodontia yunnanensis* (Schizoporaceae, Hymenochaetales), a new species from southern China. Annales Botanici Fennici 58(4–6): 259–266. https://doi.org/10.5735/085.058.0411

Luo KY, Qu MH, Zhao CL (2021a) Additions to the knowledge of Corticioid *Xylodon* (Schizoporaceae, Hymenochaetales): Introducing three new *Xylodon* species from southern China. Diversity 13(11): 581. https://doi.org/10.3390/d13110581

Luo X, Chen YH, Zhao CL (2021b) *Lyomyces fissuratus* and *L. fumosus* (Schizoporaceae, Hymenochaetales), new species from southern China. Annales Botanici Fennici 4(4–6): 58. https://doi.org/10.5735/085.058.0404

Luo X, Chen YH, Zhao CL (2021c) Morphological and phylogenetic characterization of fungi within Hymenochaetales: Introducing two new species from southern China. Nordic Journal of Botany 12(12): 39. https://doi.org/10.1111/njb.03414

Luo KY, Chen ZY, Zhao CL (2022) Phylogenetic and taxonomic analyses of three new woodinhabiting Fungi of *Xylodon* (Basidiomycota) in a Forest Ecological System. Journal of Fungi (Basel, Switzerland) 8(4): 405. https://doi.org/10.3390/jof8040405

Ma X, Zhao CL (2019) *Crepatura ellipsospora* gen. et sp. nov. in Phanerochaetaceae (Polyporales, Basidiomycota) bearing a tuberculate hymenial surface. Mycological Progress 18: 785–793. https://doi.org/10.1007/s11557-019-01488-0

Miller MA, Pfeiffer W, Schwartz T (2012) The CIPRES Science Gateway: Enabling high-impact science for phylogenetics researchers with limited resources. Association for Computing Machinery 39: 1–8. https://doi.org/10.1145/2335755.2335836

Núñez M, Ryvarden L (2001) East Asian polypores 2. Synopsis Fungorum 14: 165–522.

Nylander JAA (2004) MrModeltest v.2. Program Distributed by the Author; Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.

Petersen JH (1996) The Danish Mycological Society's colour-chart. Foreningen til Svampekundskabens Fremme, Greve.

Qu MH, Zhao CL (2022) *Xylodon flocculosus* sp. nov. from Yunnan, China. Mycotaxon 137(2): 189–201. https://doi.org/10.5248/137.189

Qu MH, Wang DQ, Zhao CL (2022) A phylogenetic and taxonomic study on *Xylodon* (Hymenochaetales): Focusing on three new *Xylodon* species from southern China. Journal of Fungi 8(1): 35. https://doi.org/10.3390/jof8010035

Rabenhorst GL (1851) Klotzschii herbarium vivum mycologicum sistens fungorum per totam Germaniam crescentium collectionem perfectam. Editio prima. Centuria 8: 1501–1600.

Rathnayaka AR, Tennakoon DS, Jones GE, Wanasinghe DN, Bhat DJ, Priyashantha A HAH, Stephenson SL, Tibpromma S, Karunarathna SC (2024) Significance of precise documentation of hosts and geospatial data of fungal collections, with an emphasis on plant-associated fungi. New Zealand Journal of Botany 1–28. https://doi.org/10.1080/0028825X.2024.2381734

Rehner SA, Samuels GJ (1994) Taxonomy and phylogeny of *Gliocladium* analysed from nuclear large subunit ribosomal DNA sequences. Mycological Research 98(6): 625–634. https://doi.org/10.1016/S0953-7562(09)80409-7

Riebesehl J, Langer E (2017) *Hyphodontia* s.l. (Hymenochaetales, Basidiomycota): 35 new combinations and new keys to currently all 120 species. Mycological Progress 16(6): 637–666. https://doi.org/10.1007/s11557-017-1299-8

Riebesehl J, Yurchenko E, Nakasone KK, Langer E (2019) Phylogenetic and morphological studies in *Xylodon* (Hymenochaetales, Basidiomycota) with the addition of four new species. MycoKeys 47: 97–137. https://doi.org/10.3897/mycokeys.47.31130

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Ryvarden L, Melo I (2014) Poroid fungi of Europe. Synopsis Fungorum 31: 1–455.

Viner I, Miettinen O (2022) *Lyomyces denudatus*, a new species with a disjunct distribution. Lilloa 59: 377–385. https://doi.org/10.30550/j.lil/2022.59.S/2022.09.14

Viner I, Spirin V, Zíbarová L, Larsson KH (2018) Additions to the taxonomy of *Lagarobasidium* and *Xylodon* (Hymenochaetales, Basidiomycota). MycoKeys 41: 65–90. https://doi.org/10.3897/mycokeys.41.28987

Viner I, Bortnikov F, Miettinen O (2022) On six African species of *Lyomyces* and *Xylodon*. Fungal Systematics and Evolution 8: 163–178. https://doi.org/10.3114/fuse.2021.08.13

Wang M, Chen YY (2017) Phylogeny and taxonomy of the genus *Hyphodontia* (Hymenochaetales, Basidiomycota) in China. Phytotaxa 309(1): 45–54. https://doi.org/10.11646/phytotaxa.309.1.4

Wang XW, May TW, Liu SL, Zhou LW (2021) Towards a natural classification of *Hyphodontia* sensu lato and the trait evolution of basidiocarps within Hymenochaetales (Basidiomycota). Journal of Fungi (Basel, Switzerland) 7(6): 478. https://doi.org/10.3390/jof7060478

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR protocols: A Guide to Methods and Applications. Academic Press, San Diego, CA, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wijayawardene NN, Hyde KD, Al-Ani LKT, Tedersoo L, Haelewaters D, Rajeshkumar KC, et al. (2020) Outline of Fungi and fungus-like taxa. Mycosphere 11(1): 1060–1456. https://doi.org/10.5943/mycosphere/11/1/8

Wu SH (1990) The Corticiaceae (Basidiomycetes) subfamilies Phlebioideae, Phanerochaetoideae and Hyphodermoideae in Taiwan. Acta Botanica Fennica 142: 1–123.

Wu F, Zhou LW, Vlasák J, Dai YC (2022a) Global diversity and systematics of Hymenochaetaceae with poroid hymenophore. Fungal Diversity 113(1): 1–192. https://doi.org/10.1007/s13225-021-00496-4

Wu F, Man XW, Tohtirjap A, Dai YC (2022b) A comparison of polypore fungal and species composition in forest ecosystems of China, North America, and Europe. Forest Ecosystems 9: 100051. https://doi.org/10.1016/j.fecs.2022.100051

Xiong HX, Dai YC, Wu SH (2009) Three new species of *Hyphodontia* from Taiwan. Mycological Progress 8(3): 165–169. https://doi.org/10.1007/s11557-009-0587-3.

Yang Y, Jiang QQ, Li Q, Yang JW, Cha L, Cheng LJ, Yang SQ, Zhao CL (2023) Zhou, H.M. Molecular systematics and taxonomic analyses of three new wood-inhabiting fungi of *Hyphoderma* (Hyphodermataceae,Basidiomycota). Journal of Fungi 9: 1044. https://doi.org/10.3390/jof9111044

Yang Y, Li R, Jiang QQ, Zhou HM, Muhammad A, Wang HJ, Zhao CL (2024) Phylogenetic and taxonomic analyses reveal three new wood-inhabiting fungi (Polyporales, Basidiomycota) in China. Journal of Fungi 10: 55. https://doi.org/10.3390/jof10010055

Yuan Q, Luo KY, Zhang Y, Zhao CL (2023) Morphological characteristics and phylogenetic analyses revealed three new wood-inhabiting fungi (Agaricomycetes, Basidiomycota) in Southern China. Phytotaxa 592: 179–195. https://doi.org/10.11646/phytotaxa.592.3.1

Yurchenko E, Wu SH (2013) Three new species of *Hyphodontia* with peg-like hyphal aggregations. Mycological Progress 13(3): 533–545. https://doi.org/10.1007/s11557-013-0935-1

Yurchenko E, Wu SH (2016) A key to the species of *Hyphodontia* sensu lato. MycoKeys 12: 1–27. https://doi.org/10.3897/mycokeys.12.7568

Yurchenko E, Xiong HX, Wu SH (2013) Four new species of *Hyphodontia* (*Xylodon* ss. Hjortstam & Ryvarden, Basidiomycota) from Taiwan. Nova Hedwigia 96(3–4): 545–558. https://doi.org/10.1127/0029-5035/2013/0092

Yurchenko E, Riebesehl J, Langer E (2017) Clarification of *Lyomyces sambuci* complex with the descriptions of four new species. Mycological Progress 16(9): 865–876. https://doi.org/10.1007/s11557-017-1321-1

Yurchenko E, Riebesehl J, Langer E (2020) *Fasciodontia* gen. nov. (Hymenochaetales, Basidiomycota) and the taxonomic status of *Deviodontia*. Mycological Progress 19(2): 171–184. https://doi.org/10.1007/s11557-019-01554-7

Yurchenko E, Riebesehl J, Viner I, Motato-Vásquez V, Miettinen O (2024) *Xylodon lanatus* complex and other additions to *Xylodon*. Mycological Progress 23: 9. https://doi.org/10.1007/s11557-024-01947-3

Zhang XC, Li YC, Wang YY, Xu Z, Zhao CL, Zhou HM (2024) *Xylodon asiaticus* (Hymenochaetales, Basidiomycota), a new species of corticioid fungus from southern China. Phytotaxa 634: 1–15. https://doi.org/10.11646/phytotaxa.634.1.1

Zhao CL, Wu ZQ (2017) *Ceriporiopsis kunmingensis* sp. nov. (Polyporales, Basidiomycota) evidenced by morphological characters and phylogenetic analysis. Mycological Progress 16: 93–100. https://doi.org/10.1007/s11557-016-1259-8

Zhao CL, He XS, Wanghe KY, Cui BK, Dai YC (2014) *Flammeopellis bambusicola* gen. et. sp. nov. (Polyporales, Basidiomycota) evidenced by morphological characters and phylogenetic analysis. Mycological Progress 13: 771–780. https://doi.org/10.1007/s11557-014-0960-8

Zhao CL, Chen H, Song J, Cui BK (2015) Phylogeny and taxonomy of the genus *Abundisporus* (Polyporales, Basidiomycota). Mycological Progress 14: 38. https://doi.org/10.1007/s11557-015-1062-y

Zhao CL, Wu F, Dai YC (2016) *Leifiporia rhizomorpha* gen. et sp. nov. and *L. eucalypti* comb. nov. in Polyporaceae (Basidiomycota). Mycological Progress 15: 799–809. https://doi.org/10.1007/s11557-016-1210-z

Zhao CL, Qu MH, Huang RX, Karunarathna SC (2023) Multi-Gene Phylogeny and Taxonomy of the Wood-Rotting Fungal Genus *Phlebia* sensu lato (Polyporales, Basidiomycota). Journal of Fungi 9: 320. https://doi.org/10.3390/jof9030320

Zhou Q, Jiang QQ, Yang X, Yang JW, Zhao CL, Zhao J (2024) Phylogenetic and taxonomic analyses of five new wood-inhabiting fungi of *Botryobasidium*, *Coltricia* and *Coltriciella* (Basidiomycota) from China. Journal of Fungi 10: 205. https://doi.org/10.3390/jof10030205